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BIOLOGICAL BULLETIN

THE FINDING OF THE QUEEN OF THE ARMY ANT *ECITON HAMATUM* FABRICIUS[1]

WILLIAM MORTON WHEELER.

After the peculiar, large-bodied, wingless females, or queens of the army ants of the American tropics belonging to the typical subgenus Eciton had been sought in vain for many years by many collectors I finally succeeded in July, 1920, in securing two queens of *Eciton burchelli* Westwood in British Guiana, and the same year published an account of their capture.[2] Since that time the queens of three other typical Ecitons have been discovered in rapid succession. In August, 1920, Mr. F. M. Gaige took the queen of *E. vagans* Roger in Colombia, but has not yet described the specimen. In 1923 Dr. Carlos Bruch published an account with fine figures, of a queen of *E. dulcius* Forel, subsp. *jujuensis* Forel, which he took in the Argentine.[3] He has also described a queen of *Eciton hetschkoi* Mayr, captured by Weiser in July 1923 in the same country.[4] The latter is not, however, a *true* Eciton, but belongs to the subgenus *Acamatus*, which occurs also in our Southern United States, from which I have described the queens of three species (*schmitti* Emery, *opacithorax* Emery and *carolinense* Emery). More recently Reichensperger has published a description of the queen of *E. quadriglume* Haliday, from four specimens taken by Franciscan brothers on the Rio Negro, Brazil in the fall of 1923.[5] This *Eciton* is very closely related to

[1] Contributions from The Entomological Laboratory of the Bussey Institution, Harvard University, No. 244.

[2] "Observations on Army Ants in British Guiana," *Proc. Amer. Acad. Arts and Sci.*, 56, 1921, p. 291–328, 10 figs.

[3] "Estudios Mirmecológicos," *Rev. Mus. de la Plata*, 27, 1923, p. 172–179, 1 pl. 8 text-figs.

[4] "Descripción de la reina '*Eciton* (*Acamatus*) *Hetschkoi*' Mayr," *Rev. Soc. Argent. Cienc. Nat.*, 7, 1924, p. 232–235, 2 pls., 4 figs.

[5] "Das Weibchen von *Eciton quadriglume* Hal., einige neue ecitophile Histeriden und allgemeine Bemerkumgen," *Zool. Anzeig.*, 60, 1924, p. 201–213, 5 figs.

dulcius. Among the few remaining species of true *Eciton* of which the queen has persistently eluded capture is *E. hamatum*. During the past summer (1924) I was fortunate enough to secure a beautiful specimen of this insect from a bivouacking colony just behind the new tropical laboratory on Barro Colorado Island in the Panama Canal Zone. This find is, perhaps, the more important because *hamatum* is the type of the genus and because it has such a wide distribution (from Brazil to Mexico) and is so common that its raids have been noticed by nearly every zoological explorer in tropical America. It is, in fact, among the more than one hundred described species of *Eciton*, the one which has been longest known and most often cited in the literature since Fabricius first described the soldier in 1781.

At 8.00 A.M. on August 1st, after a heavy rain on the preceding day, while collecting behind the laboratory I encountered an army of *Eciton hamatum* foraging along the central trail (Fig. 1) and in the adjacent jungle. The workers were plundering numerous nests of ants (*Pheidole*, *Acromyrmex* and *Camponotus* species) and carrying away their helpless larvæ and pupæ. On one of the tall trees they had found a large nest of a yellowish wasp (*Polybia* sp.) and for some hours were bringing in the brood in great quantities. Dr. Curt Richter devoted the morning to watching the files, computing their rate of movement and the nature of their prey. By following the various converging columns we eventually located the colony which was bivouacking less than a hundred yards from the laboratory near the edge of the jungle. The great mass of ants presented an astonishing spectacle (Fig. 2). They had selected the base of a small tree, which, about 15 inches above the ground, was joined to the trunk of a young stilt palm by a looped liana and some twigs, together forming a horizontal frame. The larger tree trunk was inclined to the north so that the surface of the bark and the ground beneath were quite dry. In this spot, which had evidently been sheltered from the heavy rains for several days, the ants had congregated in a compact, cuboidal mass, 13 to 15 inches high and broad, and suspended from the frame above mentioned. Dozens of large workers hung by their claws from the twigs and supported solid clusters and curtain-like sheets of workers and soldiers, the

FIG. 1. Entrance to the central trail through the jungle on Barro Colorado. The Ecitons were foraging along this trail. Their suspended swarm (shown in Fig. 2) was situated in the jungle a few hundred feet to the left. Photograph by Dr. David Fairchild.

latter dotting the somber mass of intertwined brown-red bodies, legs and antennæ with their large shining, ivory-white heads. The mass hung down to the ground but left a small opening at the bottom on the west side, a kind of portal, through which the

FIG. 2. Bivouacking colony of *Eciton hamatum*. The minute white dots are the heads of the soldiers scattered through the suspended mass of workers. Photograph by Dr. Frances G. Smith.

converging bootyladen files of workers and soldiers were continually pouring to deposit their burdens in the center of the mass and on the ground immediately beneath it.

At my request, Miss F. G. Smith, who happened to be visiting the laboratory, kindly undertook to photograph the colony, and later Dr. Fairchild took a more enlarged flash-light picture. Considering the fact that the ants were clustered in a dark spot, the two photographs, which are shown in Figs. 2 and 3, give a good likeness of the shape of the cluster and of its composition. The blurred areas in Fig. 3 are, of course, due to the movements of several workers on its surface.

FIG. 3. Part of the suspended bivouacking colony of *Eciton hamatum* Fabr. on Barro Colorado Island. The interlacing legs and antennæ of the thousands of ants are distinctly shown. The white spots are the heads of the soldiers scattered among the swarm. About ½ natural size. Photograph by Dr. David Fairchild.

Throughout the day the colony showed no essential change. It seemed very probable that the queen was concealed somewhere in the cluster, and although my enthusiastic young friend, Dr. Richter, wished to keep the colony under observation for several days, if possible, my arguments, inspired by fear that it might decamp during the night and disappear in the jungle and a desire

FIG. 4. Soldier and small worker of *Eciton hamatum* Fabr. Photograph by Dr. David Fairchild.

to secure the unknown female and any guests, or ecitophiles that the mass might contain, eventually convinced him and my other companions, Mr. Nathan Banks, Dr. David Fairchild, his son Graham, and Mr. Frederick Burgess that it would be advisable to kill the whole mass and sort it over carefully at our leisure. The opportunity was, indeed, exceptional, because bivouacking colonies of army ants are rarely seen and when one is encountered it is almost always in some inaccessible place, in or under a large log, in a hollow tree-trunk or a hole in the ground. The destruction of the colony, however, seemed to be a serious matter, both because it involved eliminating one of possibly only a few

colonies of the species on the island, which is an animal and plant reservation, and because it is not an agreeable task to tackle a populous colony of one of the larger Ecitons. Fortunately *hamatum* is far from being as vicious or from stinging as badly as *E. burchelli*, though the soldiers (Fig. 4) are able to run their recurved mandibles into one's skin in such a manner as to make them as difficult to remove as an equal number of fish-hooks.

Just before dusk we matured and carried out the following plan: A towel saturated with ether was tightly wedged into the bottom of a five gallon gasoline tin from which the top had been removed. After cautiously cutting away the main supports of the framework of twigs, the tin was suddenly inverted over the mass of ants, and at the same time one of the party sprayed those left outside the receptacle with "Komo," a preparation used for killing house-flies and mosquitoes. The whole mass of asphyxiated insects, which measured two and one-half gallons, and comprised many thousands of individuals, was then examined. The queen was found, together with a great number of nearly full grown worker larvæ, but no pupæ, a considerable amount of prey, mainly ant and wasp larvæ and pupæ, and a series of interesting ecitophiles. On the following morning the *hamatum* workers and soldiers, which had been out foraging when the main body of their colony was captured, were found to have formed four small compact clusters, each about the size of an orange at widely separated points in the jungle. As usual under such circumstances these meager remnants of a vigorous population had a demoralized and dejected appearance. In the course of a few hours they decamped and disappeared in the undergrowth.

The *E. hamatum* queen (Figs. 5, 6 and 7) measures 15 mm. (head, thorax and petiole 6.5 mm., gaster 8.5 mm.) and differs from the queen of *E. burchelli* Westwood in the following particulars: The color is uniformly ferruginous red, of a distinctly paler tint than in *burchelli*, and there are no markings on the gaster, except some brownish clouds on the middle of the second to fourth segments, near their posterior borders, and a few brownish spots on the fifth segment. The mandibles are shorter and slightly broader, the antennal funiculi longer and stouter, the cheeks more inflated, the antennal foveæ larger and more sharply

FIG. 5. *Eciton hamatum* Fabr. Female, dorsal view. Photograph by Prof. C. T. Brues.

FIG. 6. *Eciton hamatum* Fabr. Female, dorsolateral view. Photograph by Prof. C. T. Brues.

defined and the eyes slightly larger than in *burchelli*. The pronotum is longer and more narrowed anteriorly, the mesonotum less convex and not distinctly grooved in the middle, the tubercles

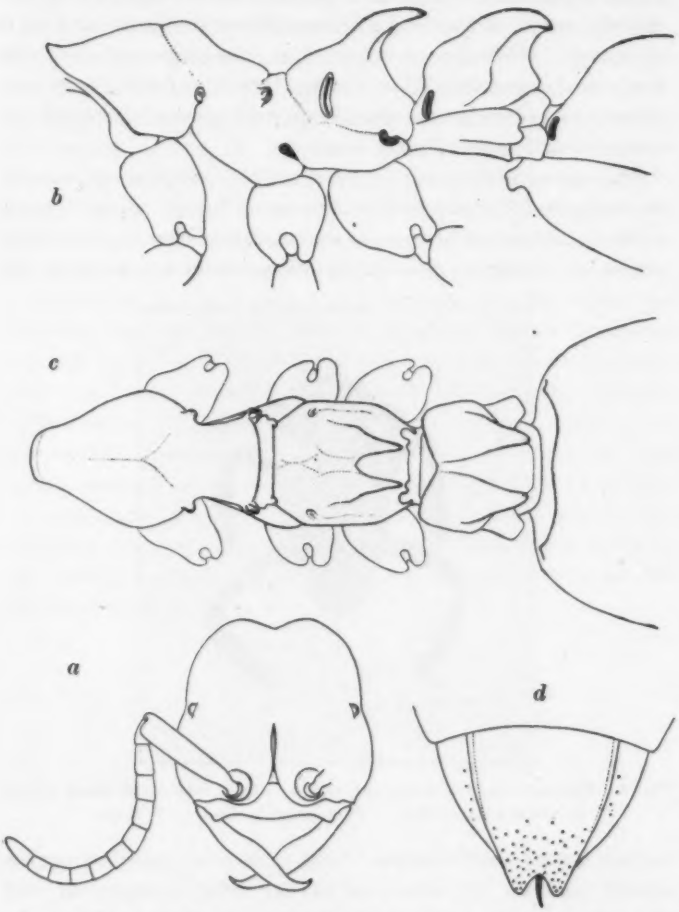

FIG. 7. *Eciton hamatum* Fabr. female; *a*, head, dorsal aspect; *b*, thorax and petiole in profile; *c*, same, dorsal aspect; *d*, hypopygium.

on the sides of the metanotum more pronounced. The horns on the epinotum are much longer and more pointed, those on the

petiole much shorter, blunter and more rounded than in Westwood's species. The surface of the body, even of the sides of the epinotum and petiole are subopaque, the coarse punctures on the thoracic dorsum are much as in *burchelli*, but those on the convex dorsal portion of the first gastric segment are larger and more scattered. The hairs are shorter, finer, less golden and decidedly less abundant, especially on the legs, which in *burchelli* are very pilose. Other structural details may be gleaned from the accompanying figures (Figs. 5, 6 and 7).

This queen is obviously in the same physiological stage as the two queens of *E. burchelli* described in my former paper. Owing to the small size of her gaster she must be either a young individual or, if the mother of the numerous larvæ, workers and

FIG. 8. Histerid ecitophile *Euxenister wheeleri* Mann, from bivouacking colony of *Eciton hamatum* Fabr. Photograph by Prof. C. T. Brues.

soldiers among which she was living, must have passed through a fecund period. The freshness of her color, integument and pilosity seems to support the former alternative. That the colony from which she was taken was not as large as some *hamatum* colonies I have seen, might also indicate that she was a young individual or one in which the gaster had temporarily returned to a contracted state after a first period (perhaps seasonal) of fecundity.

Of the eleven species of insects found in the bivouacking mass of *hamatum* workers and soldiers nine are Coleoptera, one a large Thysanuran (*Atelura* sp.) and one a mite resembling *Discopoma*. The beetles have been studied by Dr. W. M. Mann and Mr. H. S. Barber of the National Museum. The former writes me that there are five species of ecitophiles, namely two Staphylinids and three new species of Histeridæ. One of these is a *Troglosternus*, one a *Synodites* and the third, the remarkable form represented in Fig. 8, has been described by Dr. Mann as *Euxenister wheeleri*. The four remaining forms are bark-inhabiting or fungus beetles which were evidently brought in as prey by the foraging columns of ants. Mr. Barber identifies the specimens as a species of *Staphylinus* (*sensu lato*), two species of *Erchomus* and a *Rhymbus* (Endomychidæ). He sends the following note concerning the last, of which several specimens were taken: "The *Rhymbus* seems to be *Rh. hemisphæricus* Gerst. 1858, but not the species treated under that name by Gorham 1873 (Biol. C–A) although his *piceus* is perhaps a synonym of Gerstäckers species. Unfortunately an earlier generic and specific name (*Bystus coccinelloides* Guérin 1857, from Colombia) is listed under *Rhymbus* Gerst. 1858, and from its original description I cannot see why this latter name should not apply to the Barro Colorado specimens. The species is new to the National Collection."

A NEW GUEST-ANT AND OTHER NEW FORMICIDÆ FROM BARRO COLORADO ISLAND, PANAMA.[1]

WILLIAM MORTON WHEELER.

The researches of the past twenty-five years have shown that the number of ants which regularly live in more or less intimate symbiotic or parasitic relations with other ants is considerable, and that the behavior exhibited under these conditions is remarkably diverse. Until recently, however, such social parasites were known only from north temperate and subtropical regions. Several very interesting forms have now been discovered in the tropics and even in the south temperate zone. The following is a list of the workerless parasites (permanent social parasites) resembling the European *Anergates atratulus* Schenck and the North American *Epœcus pergandei* Emery that have been described from paleotropical and neotropical localities:

(1) *Wheeleriella wroughtoni* Forel (1910, 1911), described from female and male specimens found living in the nests of *Monomorium solomonis indicum* Forel at Poona, India.

(2) *Parapheidole oculata* Emery (1900, 1914–15), described from a female specimen from Madagascar and supposed to be a workerless parasite of some species of *Pheidole*.

(3) *Anergatides kohli* Wasmann (1915). Males and females taken in nests of *Pheidole megacephala melancholica* Santschi in the Belgian Congo.

(4) *Plagiolepis* (*Anoplolepis*) *nuptialis* Santschi (1917). Males taken in Cape Province by Dr. H. Brauns in nests of *P.* (*A.*) *custodiens* Sm.

(5) *Pseudoatta argentina* Gallardo (1916). Female and male described from specimens taken in Argentina and supposed to be parasitic in the nests of some fungus-growing ant of the genus Mœllerius, probably *M. balzani* Emery.

(6) *Xenometra monilicornis* Emery (1917, 1921), described

[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 241.

from female specimens taken on the island of St. Thomas, W. I., in a nest of *Cardiocondyla emeryi* Forel.

(7) *Bruchomyrma acutidens* Santschi (1923), described from female specimens taken by Carlos Bruch in Argentina in the nest of *Pheidole strobeli richteri* Forel.

Besides the accounts of these extreme, workerless, permanent parasites numerous scattered and more or less incomplete notes have been published on other types of social parasites within the tropics. No slave-making ants have been recorded, but certain African and Malagasy species of Crematogaster of the subgenera *Oxygyne* and *Atopogyne* are probably temporary parasites in the nests of species of the typical subgenus Crematogaster, and the phenomenon known as "parabiosis," as Forel (1898), Mann (1912), and I (1913, 1921a) have shown, is well-developed among certain neotropical ants belonging to several genera (*Dolichoderus*, *Crematogaster*, *Odontomachus*, *Camponotus*). There is, moreover, in the tropics of both hemispheres a long series of tiny "thief," or lestobiotic ants, which belong to the Myrmicine genera *Solenopsis*, *Oligomyrmex*, *Aëromyrma*, *Pœdalgus*, *Carebara*, *Erebomyrma*, *Tranopelta*, *Liomyrmex*, *Pheidole*, *Xenomyrmex*, *Monomorium*, etc. and live in or very near the nests of other ants or of termites.

During late July and early August, 1924, while studying the exuberant ant-fauna about the new tropical laboratory on Barro Colorado Island, in the Panama Canal Zone, I repeatedly came upon a small and peculiar *Megalomyrmex* living in the fungus gardens of a *Sericomyrmex*. Since the behavior of these insects represents a new type of symbiosis or xenobiosis, I here describe them, prefacing my account of each with a few historical notes. The taxonomic descriptions of the two ants and of some small lestobiotic species associated with the *Sericomyrmex* colonies are placed at the end of the paper.

Our knowledge of the habits of the Attine ants of the genus *Sericomyrmex* is rather meager. The earliest and best account is that of Urich published as early as 1895. It refers to a Trinidad species, later described as *S. urichi* Forel, but at the time of Urich's writing supposed to be *opacus* Mayr. "The nests of these ants," he says, "are found commonly about Port of Spain, in gardens, in the grass as a rule, but sometimes in the flower beds,

and from their peculiar raised entrance can readily be recognized. They are always excavated in clayey soil, and the raised entrances, which are more or less cylindrical, are constructed with the particles of earth resulting from their mining operations and are about an inch in height. In young colonies this entrance leads into a small chamber, about six inches below the surface of the ground, situated, not at the end of the gallery but either to the left or right of it. As the colony increases the ants do not enlarge this original chamber, but, piercing its side, form another chamber near it with a small entrance hole. In large colonies, which never consist of more than about 200 individuals, a nest consists of two or three chambers which open on the original excavation. This is no longer used for growing the fungus in, but forms a sort of antechamber which generally contains material brought in by the ants to grow their mushrooms on, which is deposited here and gradually made use of. The chambers adjoining are more or less round, with a diameter of about 2–3 inches, and any small roots of plants growing through them are not cut away but used by the ants to hang their mushroom gardens on. These fill the interior of the chamber and consist of a gray spongy mass consisting of a great number of little irregular cells and resembling a coarse sponge, amongst which are scattered larvæ, pupæ, and ants. The walls of the cells consist of small round pellets resembling dust shot and are penetrated by and enveloped in white fungus hyphæ, which hold the mass together. Strewn thickly upon the surface of the garden are to be seen round white bodies about a quarter of a millimeter in diameter. These are what Möller terms "Kohl-rabi" clumps, and consist of an aggregation of hyphæ with spherical swellings on their ends. It is on this that the ants feed. The fungus found by Möller in the nests of the Brazilian fungus growers (*Acromyrmex*) is the *Rozites gongylophora* Möller, and if it is not the same species cultivated by *S. opacus* it is, at any rate, very nearly related to it. As material to grow their mushrooms on the ants make use of particles of fruit, flowers, and leaves, but prefer the fruit. They do well in artificial nests and are easy to watch. I have tried them with all kinds of vegetable products; they have taken orange, banana, rose petals and leaves, and once they even made use of the dried glue from the back of an old book

lying near their nest, but that day they had nothing else; if the choice be left to them they invariably take fruit and seem to prefer the orange among these. Very small particles of the white skin of the oranges are torn off, and, after undergoing a slight kneading process in the ants' mandibles, are placed in the nest. The neutres are all of the same size, varying but slightly and never exceed 4 mm. in length. They are more diurnal in their habits than other species of fungus growers, but also work a little at night. I have found winged forms in the nests in the month of July."

The following year Forel, while recording his observations on the Attini of Colombia, published the following remark (1896, p. 406): "The fungus gardens of the large *Atta* species, of the subgenera *Trachymyrmex* For. and *Mycocepurus* For., as well as of the genus *Sericomyrmex* were previously unknown and were discovered by me. The gardens of the three latter groups seem to resemble those of *Apterostigma*, and these small ants are never seen on the trees in the act of cutting leaves. They bring into their nests small, desiccated vegetable particles; their fungus garden lies very deep in the earth and is very imperfect." The Colombian species of *Sericomyrmex* (*S. diego* Forel) observed by Forel was not described till 1912 (p. 193). He then added the following note: "Don Diego, at the foot of the Sierra Madre de Santa Marta, Colombia, the third of March, 1896, in the forest; nest in the humus, with a crater of coarse granules. A beautiful fungus garden at a depth of 2 decimeters in the earth. The worker feigns death like the species of *Cyphomyrmex*. They collect little green vegetable particles resembling an alga and make their fungus garden of them and other débris." Essentially the same account was published by Forel in the "Biologia Centrali-Americana" (1899–1900, p. 37).

It will be noticed that Urich and not Forel was the first to observe the fungus gardens of *Sericomyrmex* and that the latter's various accounts contain some glaring discrepancies. In one account the garden is described as "very imperfect," in another as "beautiful." Furthermore, he could not have seen the fungus garden of *Mycocepurus*, which cultivates a peculiar fungus very similar to if not the same as the *Tyridiomyces formicarum* cultivated by *Cyphomyrmex rimosus* (Wheeler, 1907, p. 771).

For many years *Sericomyrmex* has been the one genus of Attine ants which I have not had an adequate opportunity to study. These insects are local or sporadic in their occurrence and very unobtrusive and timid in their behavior. Even on the few occasions when I have encountered them I could make but a superficial examination of their nests. My note-books contain only the following jottings:

FIG. 1. Laboratory of the Institute for Tropical Research on Barro Colorado Island, in Gatun Lake, Panama Canal Zone. Photograph by Mr. James Zetek.

Dec. 15, 1911, I happened on a number of nests of a small *Sericomyrmex*, which I have since described as *S. zacapanus* (1924) on the clay banks of a small irrigating ditch in an orchard at Zacapa, a very arid locality in Guatemala. The nests had small craters 2–3 inches in diameter, which were either single or in rows, like those of *Solenopsis geminata* nests, and were covered with the ejected fragments of exhausted fungus substratum. The soil was so hard that I could not reach the chambers and gardens which must have been some distance beneath the surface. The few workers that were abroad were bringing in small vegetable

particles. During the summer of 1920 I examined some of the colonies of *S. urichi*, which were nesting in the lawn near Mr. Urich's laboratory in Port of Spain, but time to make a careful investigation was lacking. During the same summer I took in the sandy area adjoining the Tropical Laboratory of the New York Zoölogical Society at Kartabo, British Guiana, a few workers of a *Sericomyrmex* which I have recently described as *impexus* (1924), but I failed to reach the chambers in the very few nests that were excavated.

My sojourn on Barro Colorado Island finally yielded the desired opportunity to study not only *Sericomyrmex* but also several other Attini. During the height of the rainy season this locality is a veritable myrmecological and mycological paradise. Within a few hundred yards of the laboratory (Fig. 1) numerous colonies of at least 14 species of fungus-growing ants could be found, all with their gardens close to the surface of the ground and easily accessible. I recognized two species of *Atta*, one of *Acromyrmex*, three of *Trachymyrmex*, three of *Apterostigma*, three of *Cyphomyrmex*, one of *Myrmecocrypta* and one of *Sericomyrmex*. Thus nearly all the known genera of Attini were represented. Further search will probably reveal the presence of *Mycocepurus* on the island. Nor were the ants the only fungus-cultivating insects. The trunks of the trees that had been felled during the dry season (spring of 1924), when the small clearing was made around the laboratory, had reached a stage when they attracted thousands of ambrosia beetles of the family Platypodidæ. During June and July these insects were everywhere making their long tubular fungus-lined galleries in the dead wood and covering the logs with their frass. It would, indeed, be difficult to find a more favorable locality for mycological investigations, not only on account of the interesting fungi cultivated by so many ants and beetles but also of the extraordinary number and variety of other fungi, which during the rainy season flourish in all parts of the jungle.

Leaving an account of the other Attini for consideration at some future time, I will here confine my remarks to the *Sericomyrmex* which harbors the *Megalomyrmex* in its gardens. This Sericomyrmex seems to represent an undescribed species, which I

shall call *amabilis*. It is very closely related to *S. impexus* Wheeler of British Guiana, but the worker is somewhat larger, the external borders of the mandibles are less convex, the mesothoracic tubercles are more acute and the silky hairs and pubescence, especially on the upper surface of the body, are longer and more conspicuous. The worker averages a little over 3 mm. in length, the female somewhat more than 5 mm., the male about 3 mm. All the phases are ferruginous brown, the female being decidedly darker and less reddish than the worker. Like most of the smaller Attini, the workers are very timid and inoffensive. When rudely touched they at once curl up and feign death. Owing to their gentle disposition and graceful and deliberate movements they are among the most fascinating ants to observe in artificial nests.

S. amabilis is probably common in many parts of the jungle on Barro Colorado Island but I was able to detect its nests only in the recently made clearing and trails, where the red clay, which gives its name to the island, is exposed to the sunlight, and there only some hours after one of the almost daily, heavy showers. As soon as the rain ceased the silky, mouse-like workers began to bring up small pellets of earth and carefully deposit them in the form of a loose crater around the entrance, which was about 3 mm. in diameter. These craters, which are completely obliterated by each rain, are probably large and noticeable during the dry season. As soon as one approaches the nest, the excavating workers, like those of *Trachymyrmex*, either feign death and become indistinguishable from the soil or hastily withdraw within the nest entrance, so that the observer must remain motionless for several minutes before they resume their labors.

Most of the nests observed had a single crater and entrance, with a slender gallery descending more or less obliquely to a chamber about 4 to 6 inches beneath the surface, but a few large nests resembled *Atta* nests, on a very diminutive scale in having several entrances and craters and as many as 3 to 5 chambers, scattered over an area of about a quarter of a square yard. The chambers varied in size from that of a pigeon's to that of a hen's egg, and were each filled with a fungus garden which was either entirely built up on the floor and walls or partly suspended from

rootlets left intact by the ants during their excavations. The substratum of the gardens consisted of small, dull-yellow pellets of uniform size, held together and covered by a dense white mycelium, bearing minute clusters (bromatia) of spherical

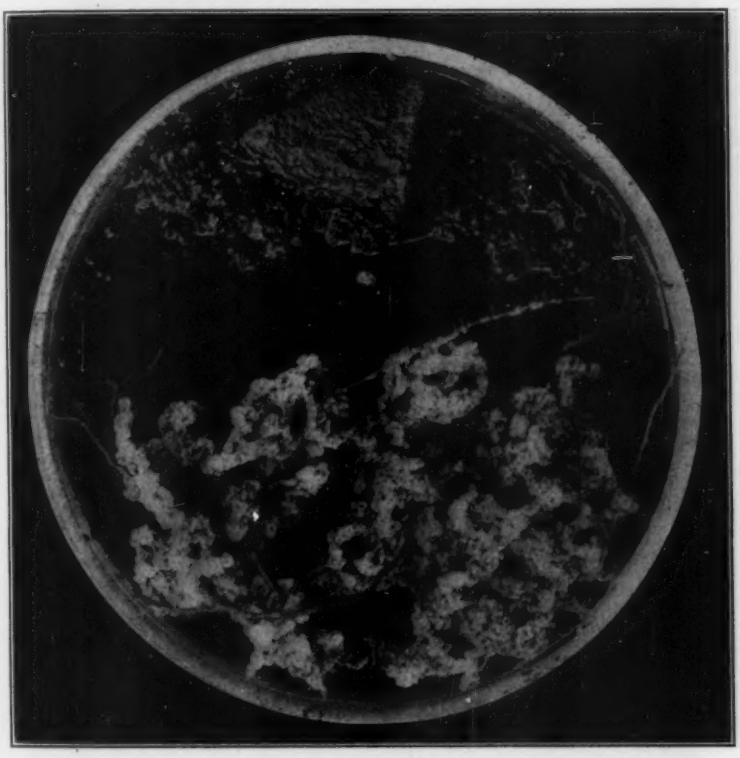

FIG. 2. Fungus garden of *Sericomyrmex amabilis* sp. nov. built in a Petri dish. × 1½. Photograph by Dr. David Fairchild.

swellings ("kohlrabi") like those of *Atta*, *Acromyrmex* and *Trachymyrmex*. Urich's description of the gardens of *S. urichi* applies accurately to those of *amabilis*. The pellets of the substratum are undoubtedly particles of soft, chlorophylless vegetable matter collected by the workers in the immediate vicinity of the nest but I was unable to identify them more closely or to observe the ants in the act of gathering them.

In order to study the ants I placed them with their brood and fungus gardens in large Petri dishes. These made excellent artificial nests in which the insects could be kept in perfect health for two to three weeks and conveniently observed under a strong pocket-lens. Within 24 to 36 hours the frail fungus gardens, which inevitably fell to pieces when extracted from the earthen chambers, were completely reconstructed by the workers as an elaborate and rather regular sponge-work with polygonal crypts a quarter to half an inch in diameter. Of course, the flat space, less than half an inch in thickness, to which the ants were confined, compelled them to rebuild their garden in the form of a disc instead of a sphere or ovoid, but this was very advantageous, since it permitted the observer to scrutinize all parts of the structure through the glass cover. (See figures 2 and 3 from photographs by my friend Dr. David Fairchild.) The ants placed their eggs, larvæ and pupæ on the fungus-covered surfaces and in the crypts. The queen is a very sluggish insect and remained for long hours in a somnolent attitude near the center of the garden, or moved about very slowly and scattered her eggs in the immediate vicinity. These were rather large and broadly elliptical and were permitted to lie where they were laid till sometime after the larvæ had hatched. The workers then carried them to other parts of the garden and placed them in contact with fresh hyphæ. Since I never saw the workers administering hyphæ or "kohlrabi" to the larvæ as described for *Atta cephalotes* by Tanner (1892), I infer that the latter, when hungry, merely reach out and crop the fungus.

The larvæ are short, thickset and beset with sparse, long, flagellum-like hairs. The head is large and subrectangular, bearing small, acute mandibles covered with acute points. This type of mandible, which I find to be peculiar to the Attini, seems to be adapted to puncturing the delicate fungus hyphæ and expressing their juices. Worker pupæ were common in the nests, but pupal males and females were much less numerous. A few of the winged adult sexual forms emerged during the last week of July and the first ten days of August.

The workers were frequently observed in the act of building and rearranging the particles of the substratum of the garden and

feeding on the "kohlrabi." They cropped the delicate hyphæ with their maxillæ, and not with their mandibles, without disturbing or shaking the substratum. On several occasions I saw

FIG. 3. Fungus garden of *Sericomyrmex amabilis* sp. nov. built in a Petri dish × 2. Photograph by Dr. David Fairchild.

them devouring injured larvæ or pupæ, and they greedily fed on the pulp of various fruits, such as mangos and bananas. They also tore off small bits of the inner rind of oranges and bananas and incorporated them in the garden. When such materials

were not available, they manured the garden with numerous golden yellow droplets of their own feces. In two of my nests the gardens were suddenly blasted in a peculiar and unexpected manner. Bits of mango had been left in the Petri dishes and had decomposed during the night. This decomposition seemed to be due to some bacterium which was accidentally transferred to the gardens, probably on the feet and mouthparts of the ants, and at once overwhelmed the fungus, so that within a few hours it shrivelled up and turned black. The ants, apparently quite unable to prevent the inroads of the lethal microörganism or to restore their fungus to its normal condition, became demoralized and eventually wandered away from it to other parts of the dishes.

The population of the *Sericomyrmex* colonies which I examined, resembled that of *Trachymyrmex* colonies, the smaller nests containing between 100 and 200, the largest (a single nest) about 300 ants. No incipient colonies were seen, but there can be no doubt that the recently fecundated queens establish their colonies and gardens in the manner described by von Ihering, Huber, Gœldi and Bruch for various South American species of Atta and Acromyrmex.

The guest-ant, which I found in ten out of the twelve Sericomyrmex nests excavated in the immediate vicinity of the laboratory on Barro Colorado Island, is obviously a species of *Megalomyrmex*, a peculiar neotropical genus established by Forel in 1884 for a Colombian ant, *M. leoninus* and now known to comprise some 15 species which range from Bolivia to Mexico. While the generic name was appropriate to the type and several other species, which measure nearly a centimeter in length, it is a misnomer for several much smaller species—*gœldii* Forel, *pusillus* Forel, *wallacei* Mann, *silvestrii* Wheeler and *sjöstedti* Wheeler—which have been recently described. The known species of the genus are divisible into two groups, one of which, including the type, has convex, coarsely 5- or 6-toothed mandibles, with a sharp angle between their apical and basal borders, whereas in the other group, comprising only two species, *silvestrii* and *sjöstedti*, the mandibles are narrower and more flattened, with a rounded angle between the basal and apical borders and the latter with two large terminal teeth and a series of very minute basal denticles. This

group is regarded by Mann as a distinct subgenus, for which he has proposed the name Wheelerimyrmex. I find that there is also a difference in the number of palpal joints in these two groups. In Megalomyrmex sens. str. (*M. bituberculatus* Fabr.) the maxillary palpi are 4-jointed, the labial palpi 3-jointed.[1] In *Wheelerimyrmex* I find the maxillary palpi to be 3-jointed, the labial palpi 2-jointed. The guest ant, which really represents a new subgenus and species and is described in the sequel as *Cepobroticus symmetochus*, has the same number of palpal joints as *Wheelerimyrmex*, but the mandibles are intermediate between the two other subgenera, having a sharp angle between the basal and apical border, and the latter with a large terminal and five or six small basal teeth. The antennæ, moreover, are short, all the funicular joints, except the last being decidedly broader than long and the clava absent. The promesonotal suture is obsolete but this character occurs also in one species of Wheelerimyrmex (*silvestrii*). In *sjöstedti* the suture is as distinct as it is in the species of Megalomyrmex *sens. str.* The eyes of the worker *Cepobroticus* are rather small.

It is, perhaps, significant that Emery (1921) has placed the genus *Megalomyrmex* in his tribe Monomorii, in the midst of a series of Old World genera—*Hagioxenus*, *Wheeleriella*, *Phacota*, *Xenomyrmex* and *Liomyrmex*—which are known to have xenobiotic or parasitic habits. Unfortunately very little is known concerning the habits of the described species of *Megalomyrmex*. The only data I have been able to secure are a few notes by Mann on *M. tuberculatus* and *M.* (*W.*) *silvestrii*. Of the former he says (1916, p. 445): "This form, which is confined to the upper Amazonian region, attends Membracidæ and the workers were generally found in company with these on shrubs in the dense forest. The nest is subterranean, the entrance nearly always at the base of a tree. The living insect is slow in its movements." Concerning *silvestrii*, which he observed in Honduras, he says: "A good series of workers were taken at Ceiba and San Juan Pueblo, nesting in the ground and in rotten logs. It is a timid species and very active when disturbed." These notes indicate that the species of Megalomyrmex *sens. str.* and the subgenus

[1] Forel and Emery give 3 joints for each palpus.

Wheelerimyrmex are nonparasitic and epigæic. The occurrence of *Cepobroticus* only as a hypogæic inquiline, or guest in the fungus gardens of *Sericomyrmex* may be regarded as an ethological character which still further emphasizes its subgeneric status.

The *Cepobroticus symmetochus* worker measures only 3–3.5 mm., the female 3.8 mm., the male 3 mm. It is therefore the smallest known species of its genus. The body is very smooth and shining in all three phases and in the worker and female yellowish red, with the appendages scarcely paler and the dorsal median third of the gaster dark brown or blackish. The male is paler and more yellow throughout. All the castes, and especially the worker and female, are covered with rather coarse, long, golden yellow hairs. For other characters the taxonomic description and figures may be consulted.

The colonies of the *Cepobroticus* so frequently found living with *Sericomyrmex amabilis* were decidedly less populous than those of their host. The largest comprised less than 75 individuals, and often the number did not exceed 40 or 50. In every nest a deälated mother queen was present. She usually took up her station, surrounded by a group of her workers, in one of the crypts of the fungus garden a short distance—half to three quarters of an inch—from the *Sericomyrmex* queen. The guest ants kept their brood in small clusters scattered through the garden and each cluster was cared for by a few workers. Although the ants and their brood were thus intermingled, the workers of each species lavished their attention exclusively on their own eggs, larvæ and pupæ and were never seen even to transport the progeny of the other species from one part of the garden to another.

The workers and queens of *Cepobroticus* are rather alert and move about more rapidly than their hosts. They devote so much time to licking and fondling one another that the observer is somewhat astonished to find them paying little or no attention to the fungus-growers. As a rule the two species are indifferent to one another. One may watch them for hours without observing anything more than rather distant, mutual antennal salutations. On rare occasions a worker *Cepobroticus* may be seen licking the gaster of a *Sericomyrmex* worker or of the sluggish queen. More

frequently one of the host workers may be observed in the act of lavishing similar but more elaborate attentions on a *Cepobroticus* worker. The fungus-grower begins by licking the feet or tarsi, the tibiæ and femora, then the thorax or abdomen and finally the head and even the mandibles of the guest. During this operation the latter remains motionless and inclines its body somewhat to one side.

The *Sericomyrmex* never feed their guests by regurgitation. This is not surprising because they never feed one another thus, but resort individually to the growing fungus bromatia. When hungry the *Cepobroticus* workers and queen also crop the fungus mycelium, but they do this rather roughly, using their mandibles and even shaking or disturbing the substratum. The guests very rarely transport or rearrange the particles of the substratum or take the slightest interest in the garden, except as a source of nourishment. Only on one occasion did I see a *Cepobroticus* carry a particle of the substratum to another spot, insert it and pat it down with her fore feet. When fresh fruit was introduced into the nest, it was much less frequently visited and eaten by the guests than by their hosts.

The larvæ and pupæ of the *Cepobroticus* can be readily distinguished from the *Sericomyrmex* brood. The larvæ are more slender and more cylindrical and have smaller heads, with flat, 3-toothed mandibles. The hairs on the body are more numerous, shorter and stouter, though rapidly tapering at their tips. I was unable to determine whether the larvæ are nourished by regurgitation or feed directly on the fungus hyphæ. The fact that they usually lie in the crypts in small clusters and in less intimate contact with the fungus than the *Sericomyrmex* larvæ would seem to indicate that they are fed by their nurses with regurgitated liquids.

The inquilines evidently lead a purely hypogæic life. Only the males and winged females leave the fungus chambers and come to the surface to mate. I took a few of the sexual forms which had thus escaped, and Prof. W. C. Allee, who collected on Barro Colorado Island during the spring of 1924, sent me among a number of miscellaneous ants a few winged females and several males of *Cepobroticus* which he had evidently taken on the ground

or vegetation. The small size of the eyes in the worker as compared with other species of Megalomyrmex indicates that this hypogæic mode of life is beginning to affect the visual organs. Other obvious adaptive characters are the dentition of the mandibles, which is well suited to cropping the fungus hyphæ, and the investment of long, golden yellow hairs, which suggest a trichomal function like the golden tufts of many symphilic myrmecophiles.

Some experiments were conducted in mingling the personnel from different *Sericomyrmex* and *Cepobroticus* colonies. The former were so gentle and tolerant that when workers and queens belonging to different colonies were placed in the same Petri dish little animosity and that of very short duration was exhibited. Similarly, when inquilines from an alien colony were introduced, they were adopted at once without hostility, but the members of different colonies of the inquilines were much more hostile to one another. Frequently workers or queens would be dragged about for days and eventually mutilated or even killed by workers of their own species. This behavior was, perhaps, to be expected from what is known of the mutual animosity of parasites of the same species when confined with a single host.

The foregoing observations make it seem probable that the *Sericomyrmex-Cepobroticus* colonies are not established by a consociation of fecundated queens of the two species immediately after their nuptial flight, but that the *Cepobroticus* queen enters a well-established *Sericomyrmex* nest in which the fungus garden is already large and flourishing and being cultivated by a lot of workers. The development of the garden by the recently fecundated *Sericomyrmex* queen, as already suggested, evidently takes place in the same manner as in *Atta*, *Acromyrmex*, *Mœllerius*, *Apterostigma* and other Attini, and is such a slow and delicate operation that the presence of a fungus-devouring inquiline at the inception of colony formation would, to say the least, seriously interfere with the welfare of both queens. On the other hand, the intrusion of the *Cepobroticus* queen at a later stage, when the garden is well established, would not seriously affect the life and development of both colonies, especially as the inquiline is by no means a very fecund ant. This is shown by the small size of her

own colony, her diminutive stature, and the small size of her gaster, which scarcely exceeds that of the worker. The fact that the workers show only a beginning in the reduction of the eyes would seem to indicate that the hypogæic and inquilinous habit is of rather recent phylogenetic origin. This supposition is also supported by the consideration that the Attini themselves constitute a young, or recent tribe of Myrmicine ants.

It is evident that *Cepobroticus* is merely a single aberrant species of *Megalomyrmex* which has abandoned an independent life, has associated itself permanently with *Sericomyrmex* and has taken to feeding on the fungus which it cultivates. The association thus established is a type of "compound nest," as defined by Wasmann, but differs from all the known types in certain important particulars. The relationship between the two species is somewhat like that obtaining between the xenobiotic *Leptothorax emersoni* and *Myrmica canadensis* in the mountains of our northern states and British America, but is in certain respects much less intimate. Although the *Cepobrotici* look after their own brood, they do not, like the *Leptothorax*, construct special chambers communicating with those of the host. Mutual feeding by regurgitation has not been developed, because both species feed on a delicate plant which is carefully provided and cultivated by one of them. We may, therefore, regard the relations of the *Cepobroticus* to the *Sericomyrmex* as a case of what the Germans call "Futterparasitismus," a case to which we might, perhaps, apply the term "mycetometochy." With the possible exception of the Pseudoatta described by Gallardo, we know of no other example of this relation among ants, but further investigation may reveal its occurrence among the termites of Africa and Southern Asia.

In the soil immediately surrounding the fungus chambers of some of the *Sericomyrmex* nests I found five minute species of ants which are described below as *Pheidole* (*Hendecapheidole*) *mendicula* sp. nov; *Oligomyrmex panamensis* sp. nov.; *Solenopsis conjurata* sp. nov.; *Tranopelta gilva* Mayr var. *columbica* Forel and *Rhizomyrma* sp. With the exception of the last these seem all to be "thief," or lestobiotic ants, but further observations will be required to establish their precise relations to the fungus

growers. The most interesting species is the *Oligomyrmex*, because no representative of this genus, which is widely distributed over the warmer portions of the Old World—Southern Europe, Asia Minor, Africa, Madagascar, India, Indonesia, Papua, Australia—has been taken hitherto in any part of the New World. The new Hendecapheidole is also of interest, because only two species of the subgenus have been described, *tachigaliæ* Wheeler and *emersoni* Wheeler (1922), both from British Guiana.

Taxonomic Descriptions.

Sericomyrmex amabilis sp. nov. (Fig. 4.)

Worker.—Length 3–3.5 mm.

Very close to *S. impexus* Wheeler but differing in its somewhat larger size and darker color and in the following structural details: The head is more deeply excised posteriorly, the eyes are distinctly larger and more convex, the posterior angles of the frontal lobes

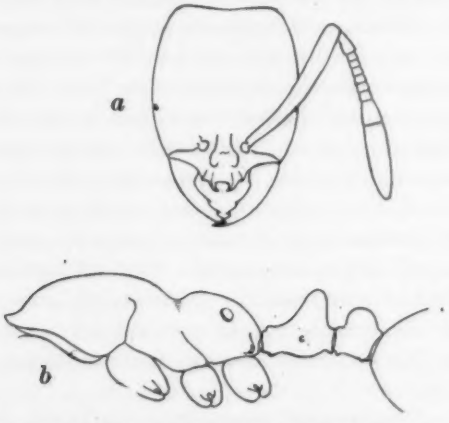

Fig. 4. *Sericomyrmex amabilis* sp. nov. *a*, head of worker, dorsal aspect; *b*, thorax and pedicel of same in profile.

more acute, the continuations of the frontal carinæ which form the inner boundaries of the scrobe-like depressions for the antennæ, more pronounced, the mandibles with less convex external borders and more pronounced striæ. Their surfaces are at the same time more shining. The median joints of the antennal

funiculi are distinctly more transverse. The thorax, abdomen and legs are very similar to those of *impexus*, but the inferior angles of the pronotum, the pair of tubercles on this segment and the two pairs of tubercles on the mesonotum are somewhat larger and more acute and the lateral marginations of the gaster are more pronounced, as are also the three broad longitudinal depressions near its base on the dorsal side.

The pilosity and pubescence are decidedly more abundant than in *impexus*. The former is longer and more completely covers the integument, the latter is also longer and more conspicuous, especially on the dorsal surface of the body. The hairs are blackish at the base, with long, slender, flexuous, pale grayish or yellowish tips. The color of the body and appendages in mature specimens is rich ferruginous brown, with somewhat darker mandibles.

Female.—Length 5–5.5 mm.; wings 6.3 mm.

Similar to the worker. Backward extensions of the frontal carinæ and of the carinæ of the cheeks more acute, so that the antennal scrobes are more strongly developed. Mandibles coarsely striatopunctate. Pronotum with a blunt tubercle on each side, the inferior angles not very distinct. Mesonotum subrectangular, slightly longer than broad, flattened above, with a feeble Y-shaped impression. Scutellum less than twice as broad as long, bluntly bidentate behind. Epinotum declivous, with a pair of blunt longitudinal ridges terminating in blunt teeth. Petiole and postpetiole each with a pair of blunt longitudinal ridges above. The large first gastric segment is broader behind than in front, with straight sides, which are marginate; the three longitudinal impressions on the dorsal surface somewhat more distinct than in the worker.

Pilosity and especially the pubescence even longer than in the worker. Color darker, more brown and less reddish. Wings rather strongly and uniformly infuscated; veins and pterostigma pale, but very narrowly outlined with blackish.

Male.—Length nearly 3 mm.

Head, including the eyes, as long as broad, somewhat narrowed behind, with straight posterior border and rounded posterior corners. Eyes rather large and convex, the ocelli small and

widely separated. Mandibles well-developed but narrow, their long apical borders finely denticulate. Antennæ slender, the scapes extending well beyond the posterior border of the head. Thorax large, the mesonotum convex anteriorly, with distinct Mayrian furrows. Scutellum trapezoidal, nearly as long as broad, feebly impressed in the middle, with entire posterior border. Petiole and postpetiole similar to those of the worker but the former more pedunculate anteriorly. Gaster small, oval; legs long and slender, the femora feebly bent.

Surface of the body smoother than in the worker and female, the mandibles and gaster somewhat shining, the remainder of the body subopaque.

Pilosity and pubescence very short and meager, only the sides of the petiole and postpetiole with tufts of hairs like those of the worker and female. Antennæ and legs destitute of hairs, with fine, indistinct pubescence.

Brownish yellow, head, a spot on the posterior portion of the mesonotum and a line on each side of it, brown. Wings colored as in the female.

Described from numerous workers, five females and a male taken on Barro Colorado Island, C. Z. during late July and early August.

This form is so close to *S. impexus* of British Guiana that it might be regarded as a subspecies. I have given it specific rank, however, because it now appears that there are several forms—*impexus* Wheeler, *urichi* Forel, *diego* Forel, *morierai* Santschi, *lutzi* Wheeler, *zacapanus* Wheeler, *opacus* Mayr, *pusillus* Forel and *aztecus* Forel—which are so closely related that they may be merely geographical races, or subspecies of one or a few highly variable species. At present our knowledge of these various forms and of their phases is so meager that it seems best to regard them as specifically distinct.

Megalomyrmex (*Cepobroticus* Subgen. nov) *symmetochus* sp. nov. (Fig. 5.)

Worker.—Length 3–3.5 mm.

Head subrectangular, very slightly narrower behind than in front, with straight posterior and very feebly convex lateral

borders the posterior corners rounded. Eyes small, feebly convex, at the middle of the sides. Minute ocelli sometimes present in large workers. Clypeus convex, its anterior border broadly and evenly rounded. Frontal carinæ short, parallel; frontal area indistinct, convex in the middle. Mandibles rather narrow and not very convex, 7–8 toothed, the apical tooth longer

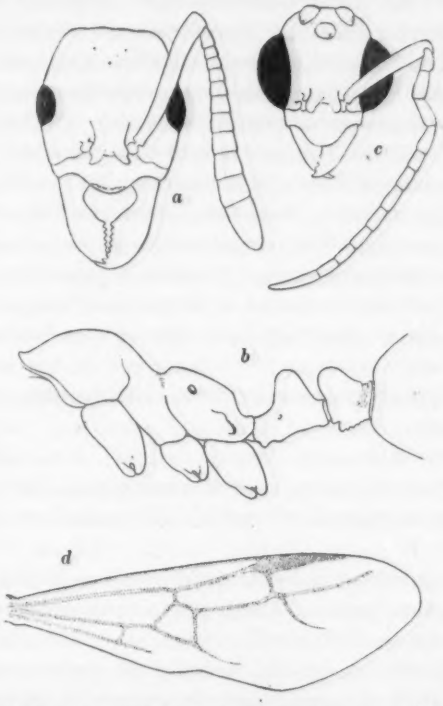

FIG. 5. *Megalomyrmex* (*Cepobroticus*) *symmetochus* sp. nov. *a*, head of worker, dorsal aspect; *b*, thorax and pedicel of same, lateral aspect; *c*, head of male, dorsal aspect; *d*, fore wing of female.

than the others which are subequal, the most basal forming the angle between the basal and apical borders. Maxillary palpi 3-jointed; labial palpi 2-jointed. Antennæ robust, the scapes extending less than one third their length beyond the posterior corners of the head; funiculi thickened apically, but not forming

a distinct club; all the joints except the first and last broader than long; joints 2–4 transverse, nearly twice as broad as long. Thorax slender, narrower than the head; the pro- and mesonotum forming an even convexity above, without promesonotal suture; the mesoëpinotal impression distinct but shallow; the epinotum in profile rising steeply for a short distance in front, then becoming straight and horizontal in the middle and gradually passing into the short sloping declivity; the metasternal angles rather large, lamellate and rounded. Seen from above the epinotum has a ridge on each side, bounding a large median longitudinal impression for the accomodation of the petiole. The latter is nearly as high as long, the peduncle shorter than the node, which rises rather abruptly in front and is rounded above, with a posterior slope like the anterior. Seen from above the node is somewhat broader than long. The ventral surface of the peduncle bears a small, blunt tooth anteriorly. Postpetiole lower than the petiole and about half again as broad, with bluntly subangular sides, the node very convex above and inclined somewhat forward. There is a small acute tooth at the anterior end on the ventral side. Gaster elliptical, its anterior border feebly excavated. Legs rather slender.

Mandibles subopaque, densely striated; remainder of body very smooth and shining, with minute, sparse, piligerous punctures. Cheeks, mesopleuræ and sides of epinotum longitudinally rugulose.

Hairs long, erect or suberect, golden yellow, somewhat bristly and rather abundant on the body, legs and antennæ; pubescence absent, except on the funiculi.

Yellowish red; mandibles, funiculi, the posterior half of the first segment of the gaster and the sutures of the thorax and pedicel, brown; tip of gaster yellowish.

Female.—Length nearly 4 mm.

Very similar to the worker, with larger eyes and distinct ocelli. Thorax as broad as the head through the eyes, the mesonotum convex and rounded above, subhexagonal, as broad as long. Epinotum sloping, without distinct base and declivity. Gaster as in the worker. Wings with a distinct discoidal cell, a single elongate cubital cell and the submarginal cell open at the tip.

Sculpture, pilosity and color as in the worker. Each ocellus with a black margin internally. Wings yellowish hyaline, iridescent, with pale yellow veins and pterostigma; their membranes distinctly pubescent.

Male.—Length nearly 3 mm.

Head without the eyes longer than broad, with rounded posterior corners and somewhat convex posterior border. Eyes and ocelli very large. Anterior border of clypeus produced and rounded. Mandibles well-developed, with triangular denticulate blades. Antennæ slender; scapes nearly as long as in the worker; first funicular joint small, as broad as long, remaining joints, except the last, subequal, twice as long as broad, terminal joint somewhat longer. Thorax resembling that of the female. Petiolar node much lower than in the worker and female. Gaster elliptical, not excavated at the base. Legs very slender.

Sculpture very similar to that of the worker and female, but the sides of the thorax are smooth.

Pilosity also similar, but the wings with longer pubescence than in the female.

Brownish yellow, gaster a little darker, antennæ and legs slightly paler; eyes and a spot along the inner border of each ocellus black.

Described from numerous workers and females and two males taken from several colonies living in the fungus gardens of *Sericomyrmex amabilis* on Barro Colorado Island, C. Z.

I have made this ant the type of a new subgenus largely on account of the dentition of the mandibles and structure of the antennal funiculus. One unfamiliar with the smaller species of *Megalomyrmex*, especially those of the subgenus *Wheelerimyrmex* would be inclined to regard the new species as a *Monomorium*, mainly because the stature is so small, the mesoëpinotal constriction so feeble and the lateral ridges of the epinotum are so poorly developed as compared with other species of *Megalomyrmex*, but I believe that there can be no doubt concerning the natural affinities of the insect. Emery states (1921) that there is no discoidal cell in the fore wing of *Megalomyrmex*, but I have found it present in all the species I have examined. Apparently this cell may be either present or absent in the species of *Monomorium*.

Pheidole (*Hendecapheidole*) *mendicula* sp. nov. (Fig. 6.)

Soldier.—Length 1.3 mm.

Head very large, subrectangular, rather convex above, about $\frac{1}{5}$ longer than broad, as broad in front as behind, with nearly straight, subparallel sides and the posterior border rather deeply and semicircularly excised in the middle. The occipital and frontal grooves are rather shallow. Eyes small, convex, sub-

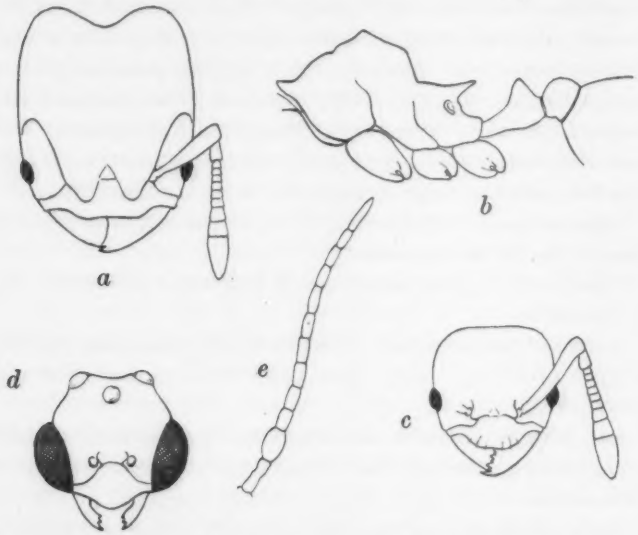

FIG. 6. *Pheidole* (*Hendecapheidole*) *mendicula* sp. nov. *a*, head of soldier, dorsal aspect; *b*, thorax and pedicel of same, in profile; *c*, head of worker, dorsal aspect; *d*, head of male; *e*, antenna of same.

triangular. Mandibles not very convex, with rather straight external borders and two large apical teeth. Clypeus somewhat flattened, its anterior border straight and entire in the middle, sinuate on each side. Frontal area small and indistinct; frontal carinæ rapidly diverging, half as long as the head and forming sharp inner borders to rather deep scrobes for the accomodation of the antennæ, which are small. Scapes reaching to the middle of the sides of the head, the club as long as the remainder of the funiculus; joints 2–7 of the latter small and transverse. Thorax

short and robust, the pro- and mesonotum forming a mass which is very convex and subangulate above in profile, the posterior surface of the mesonotum descending perpendicularly to the pronounced mesoëpinotal constriction. From above the mesonotum is semicircular in front, with rather prominent humeri, behind which the sides are straight and converge to the mesoëpinotal constriction. Epinotum as long as broad, much lower than the promesonotum, with subequal base and declivity and two backwardly directed spines which are slightly longer than the width of their bases and nearly as long as the base of the epinotum. Petiole small, about 1½ times as long as broad, the peduncle distinct and parallel-sided, the node strongly compressed anteroposteriorly, with abrupt anterior and more sloping posterior surface and entire, distinctly transverse superior border. Postpetiole nearly half again as broad as the petiole; transversely elliptical, convex and rounded above and on the sides. Gaster smaller than the head, elongate-elliptical, with slightly concave anterior border. Femora and tibiæ distinctly thickened and clavate.

Shining; mandibles and clypeus smooth and very sparsely and finely punctate. Remainder of head densely punctate and transversely rugulose, the rugules most distinct on the front. Thorax and petiole densely and finely punctate, somewhat more coarsely on the promesonotum. Postpetiole and gaster very smooth and shining, the latter with a small punctate area near the insertion of the postpetiole.

Hairs yellowish, rather long and coarse, erect or suberect, moderately numerous, longest on the abdomen, sparser and somewhat shorter on the legs.

Brownish black, mandibles, sides of clypeus, antennæ and legs piceous; tarsi brownish yellow.

Worker.—Length 1 mm.

Head as broad as long, subrectangular, with distinct but rounded posterior corners, nearly straight posterior border and feebly convex sides. Mandibles with 7 small teeth, the second, fourth and sixth from the apex very minute. Clypeal border with four or five minute denticles which are the anterior terminations of longitudinal rugules. Eyes moderately convex, as long

as their distance from the anterior border of the head. Frontal carinæ very short. There are no scrobes. Antennal scapes reaching to the posterior corners of the head. Thorax shaped much as in the soldier but the promesonotal mass is smaller and the humeral angles are less prominent, though the mesonotum is distinctly angular, with perpendicularly descending posterior surface. The epinotal spines are well developed but more erect than in the soldier. Postpetiole transversely rectangular, nearly 1½ times as broad as long and less than half again as broad as the petiole, which is similar to that of the soldier. Gaster truncated anteriorly. Legs as in the soldier.

In sculpture, pilosity and color very similar to the soldier, except that the head is merely densely and evenly punctate. The tips of the mandibles and the funiculi are paler and more brownish yellow in some specimens.

Male.—Length nearly 2 mm.

Slender; head, including the eyes, as long as broad, narrowed behind, with straight sides and concave posterior border. Eyes and ocelli large. Mandibles and clypeus small, the former tridentate, the latter convex in the middle, with rounded anterior border. Antennæ 12-jointed; scape very small and slender, scarcely longer than the swollen, ovoidal first funicular joint; joints 2–6 about twice as long as broad; 7–10 somewhat longer, the terminal joint slender and elongate. The funiculus tapers gradually to its tip. Thorax broader than the head, the mesonotum large, convex in front, as broad as long. Epinotum convex, with subequal base and declivity, rounding into each other. Petiole slender, parallel-sided, with very low and indistinct node; postpetiole somewhat broader, campanulate, as long as broad. Gaster and legs slender.

Shining; head subopaque and very finely and densely punctate; pronotum also finely punctate but more shining.

Pilosity yellowish, similar to that of the soldier and worker but shorter, especially on the legs, where the hairs are also more reclinate.

Yellowish brown; dorsal surface of body darker; head black; mandibles, mouthparts, antennæ, legs, insertions of wings and genitalia, pale yellow. Wings hyaline, with colorless veins and pterostigma.

Described from two soldiers, numerous workers and two males taken from a colony that was nesting in the soil immediately around the fungus chamber of a *Sericomyrmex amabilis* nest on Barro Colorado Island, C. Z.

This is quite distinct from the two other known species of *Hendecapheidole, tachigaliæ* Wheeler and *emersoni* Wheeler. The soldier of *mendicula* can be at once distinguished from that of *tachigaliæ* by its dark color and the very different sculpture of the head, the worker by its color and much stouter epinotal spines. The soldier *emersoni* is unknown, but the worker is paler than that of *mendicula*, much less pilose, with less developed epinotal spines. The male *emersoni* has a broader and differently shaped head, stouter petiole, coarser sculpture, darker wings and 11- instead of 12-jointed antennæ. The types of *tachigaliæ* were found inhabiting the petiolar swellings of a myrmecophyte (*Tachigalia paniculata* Aublet), those of *emersoni* a small cell within a termite nest (see Wheeler, 1921, p. 148, and 1922, p. 4).

Oligomyrmex panamensis sp. nov. (Fig. 7.)

Soldier.—Length 1.3 mm.

Head large, rather flat, fully 1⅓ times as long as broad, very slightly broader in front than behind, with straight, subparallel sides and deeply, semicircularly excised posterior border. A well-developed anterior ocellus is present. Eyes very small, situated about ⅓ the distance from the anterior to the posterior corners of the head. In the specimen the right eye is larger and pigmented, the left very minute and colorless. Mandibles short and convex, with about five blunt teeth. Clypeus very short and abrupt, its anterior border bluntly bidentate, sinuately emarginate in the middle and on the sides. Frontal carinæ short but well-developed, rapidly diverging. Antennæ small and slender, 9-jointed; the scapes reaching the lateral border of the head at points two fifths the distance from its anterior to its posterior corners. The 2-jointed club is as long as the remainder of the funiculus, the terminal joint large and swollen, fully three times as long as the penultimate, which is distinctly longer than broad; joints 2–4 subequal, broader than long; 5–6 nearly as long as broad, the basal joint as long as 2–5 together. Thorax narrower

than the head, elongate, broadest through the pronotum, which in profile is rounded in front and straight and horizontal behind, where its outline is continued into the straight, horizontal outline of the mesonotum. There is no mesoepinotal constriction but there are very small though distinct scutellar and metanotal

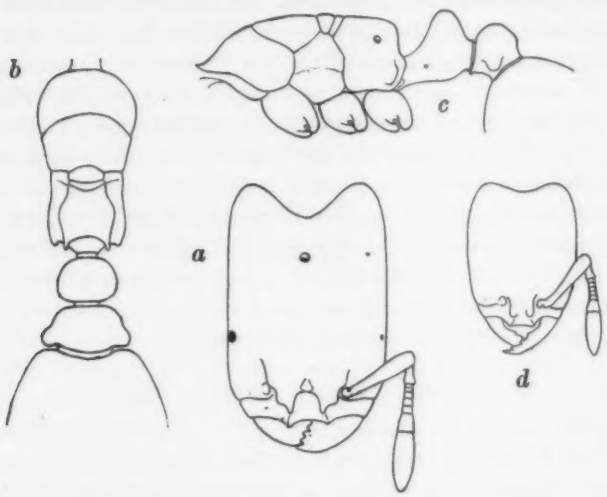

FIG. 7. *Oligomyrmex panamensis* sp. nov. *a*, head of soldier (or ergatoid?), dorsal aspect; *b*, thorax and pedicel of same, dorsal aspect; *c*, same, in profile; *d*, head of worker, dorsal aspect.

sclerites. The epinotum is subrectangular in profile, with an abrupt declivity shorter than the straight horizontal base. The angle on each side is formed by a ridge which is most distinct on the declivity. The surface between the two ridges is slightly concave. Petiole with a very short peduncle, which bears a strong, forwardly directed anteroventral tooth. The node is large and rounded, with rather steep, straight anterior and more abrupt, rounded posterior slope; from above it is transversely elliptical and nearly as long as broad. Postpetiole lower than the petiole, convex above, with a large, rounded tubercle on each side below and a minute anteroventral denticle. From above this segment is nearly 1½ times as broad as the petiolar node and of a similar shape. Gaster about the size of the head, elliptical,

somewhat flattened, its basal border rather straight. Legs short and slender.

Mandibles somewhat shining, finely punctate. Head subopaque, densely, finely and evenly longitudinally rugulose, the rugules straight and feebly diverging from between the frontal carinæ to the posterior corners. Thorax, petiole and postpetiole also subopaque but the pro- and mesonotum, and especially the scutellum, more shining; the pronotum indistinctly and very finely longitudinally striate. Gaster shining, with rather numerous, minute, piligerous punctures.

Hairs yellowish, suberect, sparse, more numerous on the gaster, fine and subappressed on the appendages.

Ferruginous red; legs, funiculi, except the articulations, and gaster paler and more yellowish; borders of mandibles and clypeus brown or blackish.

Worker.—Length 0.9 mm.

Head shaped somewhat as in the soldier, but much smaller, with evenly convex sides and more feebly excised posterior border. Eyes and ocelli absent. Mandibles less convex, with oblique blades, bearing three large apical teeth and a small basal tooth. Clypeus resembling that of the soldier. Frontal carinæ very short. Antennæ 9-jointed, the scapes reaching to the middle of the sides of the head; the terminal joint of the club proportionally longer than in the soldier, joints 2–6 of the funiculus decidedly shorter and more transverse, fully twice as broad as long. The thorax lacks the scutellar and metanotal sclerites and has a small but distinct mesoëpinotal constriction. Epinotum small, with subequal base and declivity, the former slightly convex, the latter sloping, the angle between the two obtuse and rounded. Petiolar and postpetiolar nodes subequal, the latter nearly as long as broad, rounded on the sides, without tubercles. Gaster much smaller than the head, with somewhat concave anterior border.

Smooth and shining, with scattered piligerous punctures, which are most distinct on the head, especially on its sides.

Pilosity much as in the soldier but the hairs are decidedly shorter and of more uniform length. Clypeus with four stout bristles. Hairs on the front directed transversely, on the sides of the head forward.

Yellow; legs and antennal funiculi somewhat paler.

Described from single soldier and worker specimens found in the soil surrounding a fungus chamber of *Sericomyrmex amabilis* on Barro Colorado Island, C. Z.

This minute ant, the first *Oligomyrmex* to come to light in the New World, closely resembles its Old World cousins, except in the shape of the thorax in the soldier. The fact that the eyes on the two sides of the head are differently developed indicates that it is somewhat abnormal, and since the thorax is somewhat like that of a female in possessing scutellar and metanotal sclerites the specimen may prove to be an incomplete ergatoid or pseudogyne.

Tranopelta gilva Mayr var. *columbica* Forel.

A small colony of workers with larvæ of what I take to be this form, originally described as a variety of *T. heyeri* Forel, was found in the earth immediately surrounding a fungus-chamber of *Sericomyrmex amabilis* on Barro Colorado Island. It is obviously very close to the var. *albida* Mann of Matto Grosso, Brazil, but the eyes are even smaller. The mesoëpinotal impression is a trifle less pronounced, the color is whitish as in *albida* and the pilosity is the same. It is interesting to note that Forel found the types of *columbica* at the bottom of the nest of a fungus-grower *Mycocepurus smithi* Forel. Another colony, however, was taken by him "in a subterranean nest, beneath dried cow-dung."

Solenopsis conjurata sp. nov. (Fig. 8.)

Worker.—Length 1.4–1.5 mm.

Head subrectangular, distinctly longer than broad, with feebly convex sides and slightly concave posterior border. Eyes minute, consisting of 5 or 6 abortive but pigmented ommatidia, placed one-third the distance from the anterior to the posterior corners of the head. Mandibles narrow, with oblique 4-toothed apical borders. Clypeus with the two median teeth stout, acuminate and turned inward, the lateral teeth short, broad and blunt. Antennæ rather slender; scapes reaching the posterior fifth of the head; basal funicular joint as long as the three succeeding joints together; joints 2–7 subequal, distinctly broader than long; the 2-jointed club somewhat longer than the remainder of the

funiculus; the terminal joint fully three times as long as the penultimate, which is distinctly longer than broad. Thorax rather slender, the promesonotum longer than broad, somewhat depressed above, its outline in profile rather straight in the middle; mesoëpinotal constriction distinct but not very deep; epinotum small, as long as broad, in profile convex, rounded and sloping,

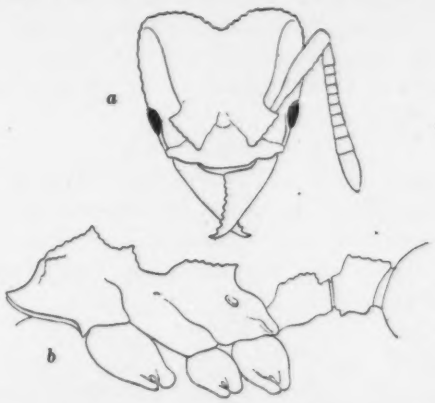

FIG. 8. *Solenopsis conjurata* sp. nov. *a*, head of worker, dorsal aspect; *b*, thorax and pedicel of same in profile.

without distinct base and declivity. Petiole small, the peduncle short, with a blunt anteroventral tooth, the node rather conical, rounded, as long as broad when seen from above. Postpetiole globular, a little broader than the petiolar node, somewhat broader than long. Gaster as large as the head, elliptical, with straight anterior border. Legs rather slender.

Smooth and shining throughout, with very fine, sparse, piligerous punctures.

Pilosity whitish, moderately long and abundant, erect on the body, more reclinate on the legs and scapes.

Uniformly pale yellow throughout, only the teeth of the mandibles reddish and the minute eyes black.

Described from numerous specimens belonging to a populous colony which was living in the earth surrounding a fungus chamber of *Sericomyrmex amabilis* on Barro Colorado Island, C. Z. These minute ants were kept for several days in an artificial

nest with the Sericomyrmex and their guest ants but though they mingled freely with the large ants remained quite unnoticed. It would seem therefore that *S. conjurata* may be a true thief-ant like many other species of the genus (*S. molesta* Say, *fugax* Latr., etc.).

I have described this Panamanian ant as new because it does not agree with any of the neotropical species of which I have seen specimens or descriptions. In Emery's key it runs down to *S. helena* Emery, but this species, judging from his figures, has a much more rectangular head and very different teeth on the clypeus.

Rhizomyrma sp.

A single pale yellow, deälated female, clearly referable to this difficult genus and measuring only 2.3 mm. was found in the same situation as the preceding species. It is very probably undescribed but it seems best not to give it a name till the cospecific worker comes to light.

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~ Taken for Journal club ~

PALM AND SOLE STUDIES.

VIII. Occurrence of Primitive Patterns (Whorls).[1]

H. H. WILDER,

Smith College.

Introduction.

If we are correct in our morphological interpretation of the friction-skin patterns of the human palms and soles (Miss Whipple, 1904; H. H. Wilder, 1916) considering them the vestiges of the former walking-pads, we should expect to find upon each of these surfaces the typical set of eleven patterns, each in its proper topographical position. These are, in either hand or foot,

Five Apical or *terminal*, upon the balls of the terminal phalanges of the five digits, fingers or toes.

Four Interdigital, upon the more distal portion of palm or sole, proximal to the bases of the separate digits, and corresponding to the intervals between them.

One Thenar, upon the thenar eminence, *i.e.*, the more proximal portion of the palm or sole, on the side of digit I., radial or tibial.

One Hypothenar, upon the hypothenar eminence, *i.e.*, the more proximal portion of the palm or sole, on the side of digit V., ulnar or fibular.

All eleven of these may be represented in a single palm or sole (H. H. Wilder, 1908, Figs. 1 and 2), but this is the greatest of rarities, only two cases, and these duplicate twins, have been thus far recorded. In the overwhelming majority of individuals the palm and sole patterns present but a small part of the complete set, and exhibit these in every stage of degeneracy down to a slight convergence of ridges in one spot, which indicates the final disappearance of the last triradius. Some of these are much more constant than others, as illustrated by the five apical patterns, the "finger-prints" of the professional dactyloscopists,

[1] Contributions from the department of Zoölogy, Smith College, No. 130.

although even here there is a well-known type, the "simple arch," in which the original pattern is reduced to its lowest terms, and shows merely the position, or "core" of the former pattern without more than the last vestiges of a single triradius. On the other hand, others, like the second interdigital of the hand, or the thenar of the foot, are seldom found, and when they do occur, it is usually in the form of a mere vestige, where the closer approximation, or the change of direction, of a few ridges, are the only indication of the former presence of a pattern that has become lost.

Again, a given pattern, when compared in different individuals in which it occurs, may show every stage of degeneracy, from a concentric whorl, the most complete and ancestral form, through those showing the loss of one or more of the triradii, to a wholly vestigial condition, where a scarcely perceptible disturbance in otherwise parallel ridges is indicative of the last traces of its presence.

In this difference in the liability of occurrence of the different patterns, and in the sort of pattern when it does occur, whether more frequently a primitive Whorl or simply a vestige, we find a perfect correlation with the physiological use of the region involved. In general those patterns which are situated upon the more prominent surfaces, and which are therefore more often in contact with external objects, are far more constant in their occurrence, and appear more frequently in the form of whorls, than are those which, during the normal course of human activities, lie in more retired spots, and are somewhat more shielded. Whorls are, for instance, by no means uncommon on the finger-balls, where a pattern of some sort is seldom entirely lacking, precisely upon those surfaces which are subject to the most wear and tear, and which press the most constantly upon external surfaces; while the four interdigitals are far less constant, and among these the second interdigital, especially protected both by the activity of the thumb, and by that of the coöperating index finger, seldom appears. On the foot the most common place for a whorl is upon the ball of the great toe (the first interdigital pattern) which bears the weight of the body at each forward step, and in the bare foot is constantly in contact with the ground.

Here the pattern is not only huge in area, and composed of coarse ridges, but is very often still in the form of the primitive whorl, composed of concentric circles, and embraced with three triradii. The thenar, on the other hand, lying on the inner side of the foot, is of all foot patterns the most obscure and frequently entirely overlooked. It seldom or never shows more than one or two triradii, and has not yet been reported in the whorl form.

In short, the correlation between the occurrence of the various patterns of the human palm and sole and their varied experiences during the customary activities of everyday life are so great that, could we suppose the entire species to become extinct, and to have left behind absolutely nothing but the records of numberless palms and soles, the customary uses of the lost hands and feet, even to the differentiation between the separate fingers, could readily be surmised and described with much detail.

While it is undeniable that this sounds strongly Lamarckian, there is nothing here intended other than to state the actual facts; whatever one's personal beliefs are with regard to the inheritance of acquired characters, it is certain that there is a strong *correlation* between the occurrence of patterns and the amount of habitual use of the regions where they occur, and between the habitual use and the percentage of occurrence of the more primitive types of patterns.

We feel that we have established the following correlations between the surface relief, the size of the ridges, the occurrence and type of patterns, and the use of the various regions of the surface.

I. Over the raised areas of the palm or sole, which come consequently into more constant contact with external objects, *i.e.*, have the hardest use:

(*a*) The ridges are the largest and coarsest.

(*b*) Patterns occur more frequently.

(*c*) The patterns show a greater percentage of whorls.

II. Over the hollowed areas, which are thus shielded from contact with external objects:

(*a*) The ridges are the finest and least prominent.

(*b*) Patterns are less likely to occur.

(*c*) When they occur they are more likely to be vestigial, *i.e.*, either arches or loops, seldom whorls.

III. In the more primitive patterns the underlying surface often presents something of the shape of a conical mound, and the center of the cone coincides with the exact center or core of the pattern. The hypothenar pattern of the hand, of frequent occurrence in the European-American race, often shows this particularly well, and in the occasional cases in which this pattern is in the form of concentric circles, it forms a definite mound, rising with each circle as one approaches the center, and at the apex is pointed, like a papilla, so that it may be noticeable in profile (Figs. 1 and 2).

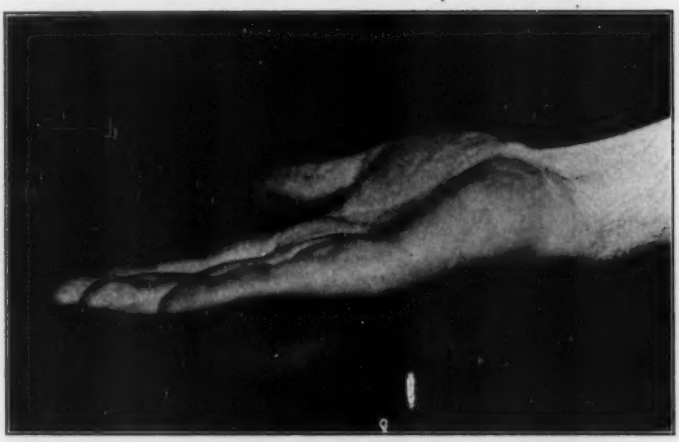

FIG. 1. Photograph of the author's right hand, seen in profile and showing the hypothenar pad covered with a whorl, plainly showing its mound-like relief and the papilla at the core of the pattern.

In spite of the great difference in the percentage of occurrence of the different morphological patterns it is probable that in the human race at the present time no one of the twenty-three patterns of the hand and foot has been allowed to degenerate so completely as never to occur in the primitive form, that of a whorl, although in the more than 1,700 individuals which I have thus far examined, there are at least three places out of the twenty-three in which such a pattern has not yet been found. These, as may be expected, are all in places where there is little contact. Two are in the foot, the thenar, and the hypothenar, and one is in the

hand, the second interdigital. Of those in the foot the thenar occurs in the hollow on the inner side of the foot, where only occasionally a piece of clay, a stone, or a wad of grass will ever

FIG. 2. A very primitive hypothenar of the right hand. Note the three embracing triradii; of these (*a*) is distal, (*b*) is the outer one, and (*c*) the proximal one, on or near the wrist.

touch this region, and the hypothenar lies on the outside, and does not meet much contact, although it would be expected, and might well be looked for in the larger Anthropoids.

Hands.

Thus, to begin with, the *apical patterns*, the ones which are found on the balls of the fingers, that is, the "finger-prints" of the identification experts, are frequently found in the form of whorls. The formulation according to the Henry system, of a given hand as 32/32, means that there is a whorl on every finger. This type is not rare in a large collection, like the one in New York, although to the professional finger-print expert a number of patterns might easily be determined as whorls, which are not typical enough for the morphologist, and would not consist of concentric circles, although they probably would have two triradii. There is some feeling that the presence of whorls upon all the fingers is a racial characteristic of the Jewish race, although definite statistics are not as yet available. Certain fingers are more apt to show whorls than others; for example the thumb and index are very apt to have whorls, while they are seldom found in the ring and little fingers. If one stop to consider the relative amount of independent use, and the variation to which they are subjected, he will see that here, also, as elsewhere, there is a direct correlation between the occurrence of whorls and the amount of use. Still, if one consult a large collection he will have little difficulty in finding even a perfect whorl on a little finger.

Morphologically we have the right to expect *four interdigital patterns*, placed along the distal border of the palm, beneath (proximal to) the four intervals between the five fingers. Occasionally we find the last two, III. and IV., beneath the separations between the middle and ring fingers, and between the ring and little fingers respectively. Thus in Fig. 3, which shows the print of the left hand of a man in New York, one of the finger-print experts at the Headquarters office, 300 Mulberry St., interdigital IV. is particularly well shown, a whorl with a center of concentric circles, and with three triradii, upper, outer, and inner. In formulating this palm either the upper or the outer of these could be used equally well as the starting point of line *D*, with an exponent letter (*t*) to signify an extra triradius. Interdigital III. is also indicated, but not so completely, and with only one triradius, the pattern being simply a loop. Fig. 4, enlarged photographically from the same, gives these same patterns in

FIG. 3. Hand-print of one of the finger-print experts in the New York office, showing the fourth interdigital in the form of a primitive whorl with three triradii. The third interdigital also is well indicated, but is not an actual whorl, and lacks two of the three necessary triradii.

more detail. In this is seen better the almost perfect condition of the fourth interdigital, with its three triradii. Fig. 5 shows a

FIG. 4. Detail taken from Fig. 3, enlarged. Here the third interdigital pattern is very typical, and compares well with the primitive hypothenar shown in Fig. 2.

detail of the right palm of the author's wife (No. 70) with interdigitals III. and IV., the first with two triradii, the latter a rudiment. In the actual hand these two areas are especially prominent, appearing almost like minute papillæ, with the patterns on their apices. In the left hand of the same individual (Fig. 6) the same two interdigitals are shown, but only one of them is a whorl, the IIId, while the IVth is simply a loop, a very common pattern in the European-American race, and almost usual enough to serve as a racial characteristic in Japanese and Chinese.

Occasionally one meets with either the third or the fourth interdigital as perfect as in Figs. 3 and 4, but it is always a surprise. My first experience of this kind was in one of two twin girls, relatives of the Director of the Eugenics Record Office at Cold Spring Harbor, L. I., but not found in her sister. This was in the right hand, and showed a whorl with three triradii, in the position of the IIId interdigital (Fig. 7). In enlargement (Fig. 8) it shows the three triradii. Fig. 9, a sketch taken with an Abbe camera, shows the details of the separate ridges. The corre-

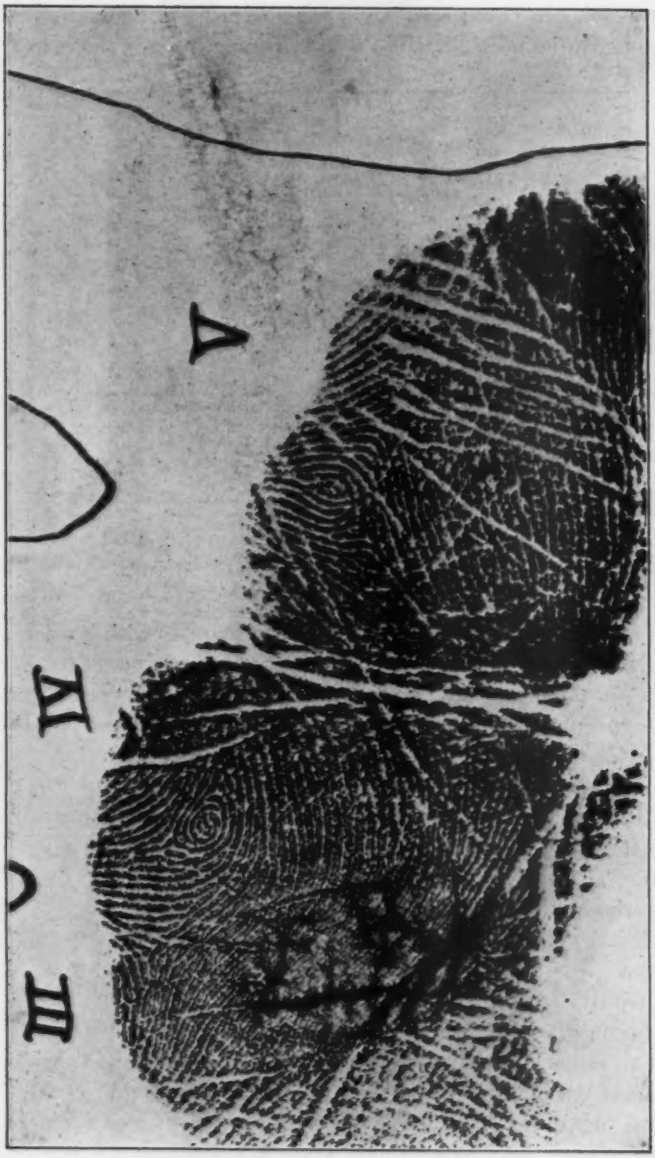

FIG. 5. Print of the distal portion of the palm of No. 70, showing interdigital patterns III. and IV., distinct but small. Compare with Fig. 6, which shows the other palm of the same individual. These show in the actual hand the same distinctness described under this other figure.

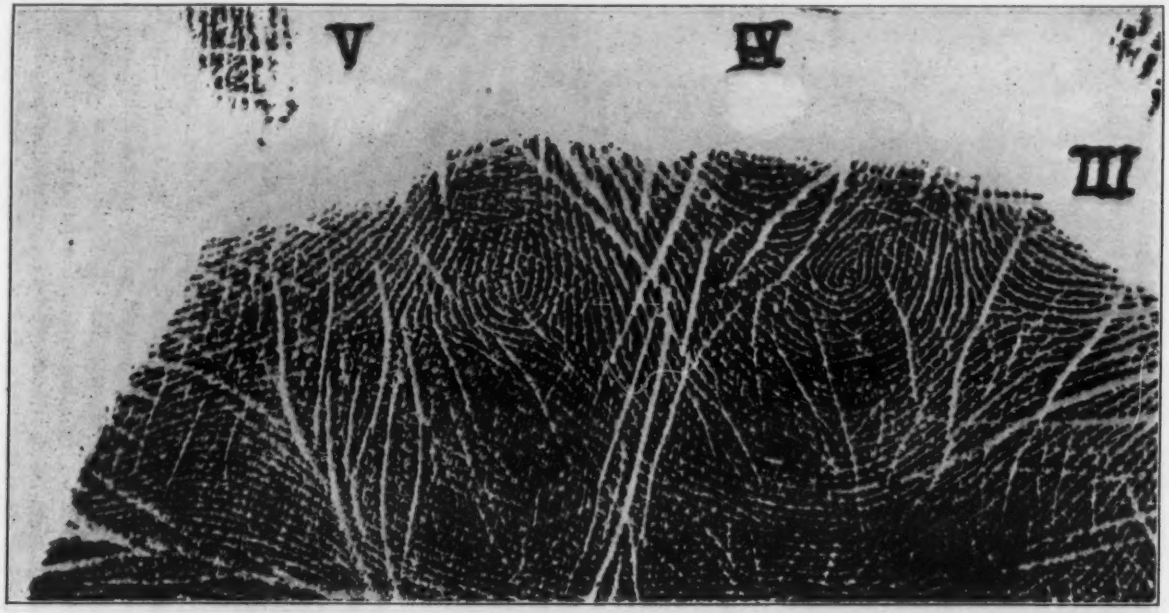

FIG. 6. Print of the distal portion of the left palm of No. 70, showing interdigital patterns III. and IV., distinct but small. In the actual palm these patterns form the apices of little low papillæ, which, when looked at across the surface of the palm, especially in the right light, appear as definite organs.

sponding IIId interdigital of the left hand of the same person (Fig. 10) shows an indication of the same pattern, but not nearly

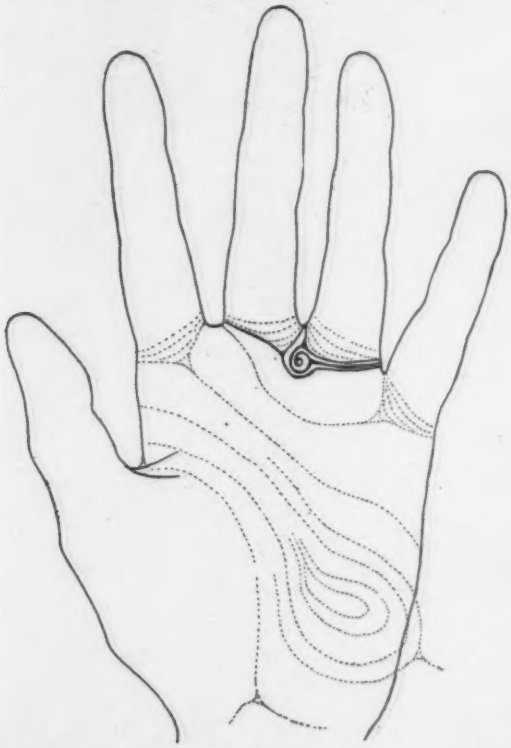

FIG. 7. Tracing of the right hand of No. 1056, with a conspicuous third interdigital pattern. The left hand of this same individual shows a good whorl on the same place (third interdigital) but smaller, and not so clear. Compare, for details Figs. 8 and 9.

as complete. Other cases of the occurrence of these interdigital patterns, the IIId and the IVth, are shown in Figs. 11 and 12, and include nearly every case I have met with. Occasionally, as in Fig. 11 the pattern is minute, but may still retain two out of the three triradii; in other cases, the pattern is still more shrunken, and can be identified only by its position on the palm, as in Fig. 12. Even here, however, in its reduced state of one

FIG. 8. Enlarged photograph of the third right interdigital pattern of No. 1056. The entire hand, with position of this pattern, is seen in Fig. 7.

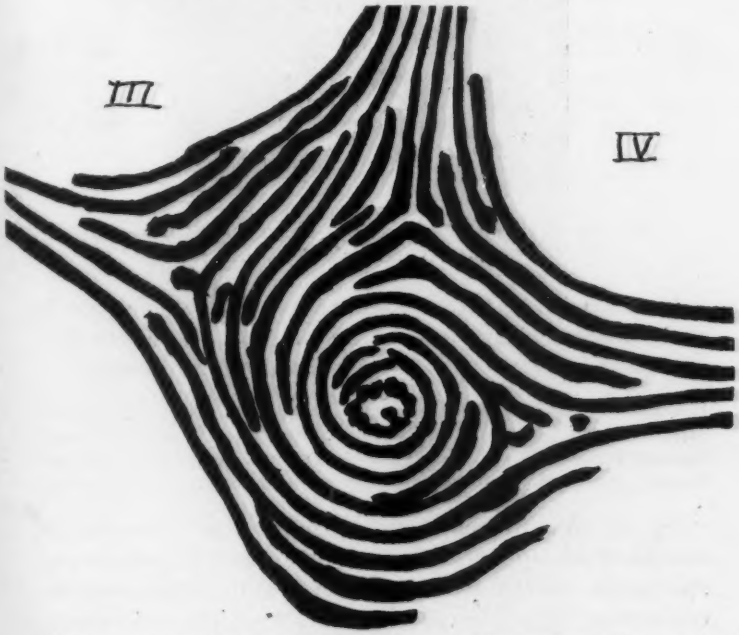

FIG. 9. Detail of the third Interdigital pattern of the right hand of No. 1056. Compare with the photograph of the same, shown in Fig. 8 and the tracing of the entire hand of Fig. 7. Drawn from an original print by a drawing camera.

ridge forming a circle, with a dot in the center, the reduction to its lowest terms, there is at least one of the three triradii, and a possibility of treating a prominent fork as another one.

FIG. 10. Photographic enlargement of the left interdigital pattern of No. 1056. Compare with Figs. 6 and 7.

Interdigital II., between the index finger and the middle one, is always rare and never more than a loop at best. In hands looked over for this very pattern, my collection gives the following:

European-Americans (females)	200 hands	5 cases
Japanese (males)	166 hands	7 cases
Japanese (females)	224 hands	2 cases
Chinese (equal number of males and females)	200 hands	1 case

Fig. 13, taken from my Japanese collection, gives as good an example of this rare pattern as I have. This hand is interesting as showing also the IIId and a rudiment of a IVth, indicated by the convergence of the ridges in the proper place. This rudimentary condition seen here is also quite likely to occur on the area designated for this pattern. Fig. 14 also from a Japanese male, shows

FIG. 11. Photographic enlargement of the fourth interdigital pattern of No. 1212. This pattern is minute, but accurately placed directly below the interval between the ring and little fingers. Of its three triradii, the upper one forms the starting point of line *D*. Line *C* has no triradius in this hand. The photograph was given by Mr. Bert Wentworth, and was taken by the owner of the hand.

FIG. 12. Photographic enlargement of the right third interdigital pattern of a female, not in my collection. This photograph was given me by Mr. Bert Wentworth.

FIG. 13. Print of detail of left hand of No. 1517, Japanese male, showing interdigital II., unusually well-developed, yet not in the form of a whorl; also interdigital III., in the form of a loop, and interdigital IV. as a vestige, with convergence of ridges in the place of the lower triradius.

the convergence of ridges quite definitely and may be considered as a case having this IId interdigital pattern in the condition of a rudiment.

FIG. 14. Detail of print of No. 1585, (Japanese male) showing vestige of interdigital II., between index and medius; also interdigital III. in the form of the more usual loop.

Hasebe finds the percentage of occurrence for this pattern as 2 per cent. among the Japanese, and 4 per cent. among the Aino, corresponding fairly well with my figures.

Interdigital I. has long been, in my experience, in the same

class as interdigital II., that is, that no whorl pattern has yet been known, but within a few years a quite perfect whorl, although small, appeared in my collection of prints of college students. The normal close association of this with the definite thenar will

FIG. 15. Tracing from the print of No. 788, a Smith College student of European-American race. This is the only case thus far known of a complete whorl in the position of the first interdigital. This has apparently the full quota of three triradii, but the triradius below, between this pattern, and the thenar, which is here, as usual, represented by a loop, evidently belongs to the thenar pattern.

be remembered, how in the majority of cases with any disturbance at all in the thenar region, there are apt to be found two loops back to back, and facing in opposite directions; the true thenar and the first interdigital. In the case in which the first inter-

digital appears as a whorl, as shown in Figs. 15 and 16, the core or center of the pattern is marked by a complete circle, beyond which there are surrounding ridges which assume the usual loop shape, and bear the usual relationship to a thenar. This is certainly not a large or conspicuous pattern, but still answers to

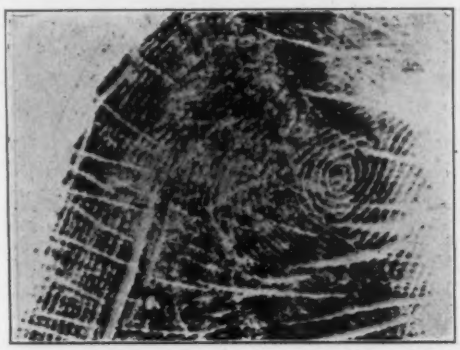

FIG. 16. Detail of the first interdigital pattern, from the left hand of No. 788, a Smith College student. This pattern here forms a complete whorl, though small. It is the only case yet reported in this position.

the requirements of a definite whorl. It is to be remembered in this case that it occurs in one of the so-called "better classes" of our own race, and that there is otherwise nothing especially primitive in this individual.

The case is a bit different in the only case of a thenar whorl which I have seen, as it occurs in a native Liberian soldier, one "Jimmy" Kamo, of the Bande tribe, collected for me by Prof. Frederick Starr (Fig. 17).

This print is in my possession and although it is very dense, as too much ink was used, it is unmistakable. By treating the print with turpentine, as may always be done in such cases, the separate ridges can be well brought out. A second case like this has been published and figured by Hasebe (his Tafel IV., Fig. 10). This author states that he has met a thenar in form of a whorl twice, both times in Japanese.

Hasebe finds the occurrence of any form of thenar pattern as 5 per cent. of all palms in both Japanese and Ainos, which may be compared with what I have found in European-Americans, 7 per

cent. in one investigation, and 11 per cent. in another. The percentage is much higher in negroes, and very much higher (50 per cent.) in Maya Indians.

FIG. 17. Tracing of the right hand of No. 571, showing a complete whorl on the thenar eminence. The subject is a Liberian soldier, Jimmie Kamo, of the Bande tribe. The print was taken by Prof. Frederick Starr.

For a time this case of the Liberian soldier, which I published in the *American Anthropologist*, 1913, p. 202, Fig. 35 was the only one known, but Hasebe has recently (1918) found a second one. Thus, with the unique case of my No. 788, the two patterns on the thenar side of the thumb, which represent the closely associated

first interdigital and the true thenar, are both occasionally represented as whorls.

Feet.

The study of toe patterns, doubtless owing to the universal deformation of the toe-balls through shoes and stockings, has scarcely been studied in this country or in Europe, but Hasebe, whose countrymen universally wear clogs (geta) which protect the plantar surface from the roughnesses of the soil, yet allow perfectly natural freedom in walking, and encourage the habit of dispensing entirely with all such artificial covering when in the house, has taken advantage of the material thus provided, and gives a careful report on the figures on the balls of the toes, the apical patterns of the foot. He studied the toes of 100 individuals (1,000 toes) and finds the distribution of whorls on the toe-balls as follows:

Right:		Left:	
1st (great)	4	1st (great)	10
2d	18	2d	13
3d	53	3d	50
4th	11	4th	12
5th	0	5th	1

Hasebe further expresses these in the form of percentages, putting both feet together, as follows:

Percentage of Whorls (both feet):	
1st (great)	7.0%
2d	15.5%
3d	51.5%
4th	11.5%
5th	.5%

From these figures there will be seen a general similarity to the condition of the fingers in respect to the occurrence of whorls, except for the small percentage in the great toe when compared with the thumb; yet we would expect this very difference when we consider the amount of difference in the habitual action of the two digits. The thumb, with its extreme flexibility, and the short and rigid great toe, show, in this difference in the occurrence of whorls, at least a correlation between use and morphology, of the same sort as elsewhere in the friction-skin configuration. The

large occurrence of whorls on the third toe is unexpected, but may be accounted for by the prominence of that digit in ordinary walking, and its extreme projection in the average foot.

FIG. 18. Apical pattern of the right great toe of a European-American.

Typical whorls do occasionally occur in the apical pattern of the great toe (Fig. 18), but a loop, usually fibular, is much commoner.

Unlike the hand, the foot, owing to the greater equality in its digits, and especially to the evenness of the intervals between them, disposes of its four interdigital patterns in a straight row across the sole, occupying the mounded region commonly spoken of as the "ball." Remembering that the first interdigital pattern is here in line with the others, and is neither dropped out of place,

FIG. 19. First interdigital (hallucal) of right foot of a Japanese girl, a student at the Doshisha school in Kyoto, showing the concentric whorl of a primitive pattern. The outer triradius was not printed but its position is indicated by the convergence of the ridges. It would doubtless have been printed if the foot had been rolled a little.

nor approximated to the thenar, as in the hand, there is occasionally a sole in which all four interdigital patterns appear as either loops or whorls, but in a number of cases, perhaps the majority, the interdigital areas except the first are not marked by patterns,

but in these cases the areas where they belong are sufficiently well indicated by the triradii, especially the upper or distal ones. The first interdigital area is often marked by a whorl, frequently a typical one (Fig. 19) but the three others are either in the form of a loop, which may open either up or down, or, perhaps most

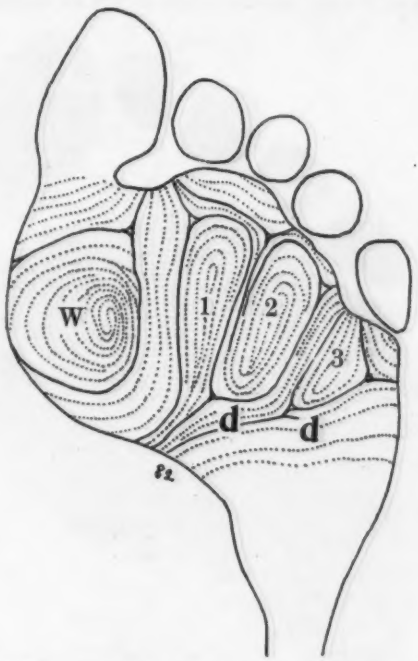

FIG. 20. Tracing from a sole print (No. 82) showing the areas of the four interdigital patterns. The first and the third are seen as whorls.

frequently of all, are crossed by approximately parallel lines with no suggestion of a pattern. The second interdigital pattern often gives the suggestion of having been squeezed laterally, and is often in the form of a narrow loop, opening downward. Aside from the first, the third interdigital is the most likely to be in the form of a whorl (Fig. 20), and in Fig. 21, there is a large whorl, concerning whose identification there is some doubt, not cleared up by the tracing of the entire sole (Fig. 22), although it is probably the fourth.

Thus, if this last be taken as the fourth interdigital, and the whorl of Fig. 20 be considered the third, which is very evident, then, with the frequent occurrence of a whorl pattern on the first interdigital, or hallucal, this leaves the second alone which has not yet been seen in the primitive form, and the squeezed up condition of this renders it very unlikely that it has in modern men any

FIG. 21. Sole print of No. 712, in which the third interdigital pattern, a whorl, is present, and large. Compare with Fig. 22, a tracing of the same sole.

longer the chance to express itself. It is quite likely that sometime the impress of a naked foot of some paleolithic man may be found on the clay floor of a European cave, and it will be then with the most breathless interest that we will look to see if the second interdigital area was then as pressed laterally as now, or whether it ever expressed itself in the form of a whorl.

There is still some little doubt concerning the identity of the proximal part of the foot, that proximal to the line of interdigital

patterns which runs across the ball, but, after the analogy of the hand the *hypothenar pattern* is to be looked for somewhere along the outer, or fibular, edge of the sole, a little back of (proximal to) the interdigital pattern of the little toe and the one next to it. There is frequently found a loop in precisely this place, which runs

FIG. 22. Tracing of the sole print of No. 712, shown in Fig. 21. The whorl is probably that of the fourth interdigital pattern.

across the entire sole, the core of which is so far out that it is usually beyond the tread area, and requires a slight outward roll of the foot to get wholly into a print. Generally, too, the loop is a narrow one, with a straight axis, but occasionally one may be met with that has a definite bend in the axis, making the loop into a hook, as in the Negro boy in Fig. 23. In one case I have found this bending of the loop so extreme that the core assumes almost the appearance of a whorl (Fig. 24). This occurred on the foot of a small son of a university professor.

The thenar pattern is to be expected on the inner side of the foot, proximal to the first interdigital pattern. This would place it on the hollow of the foot, precisely where the surface is seldom touched by foreign objects. We might expect, *a priori*, not to find the pattern developed, but to find, at most, a triradius or

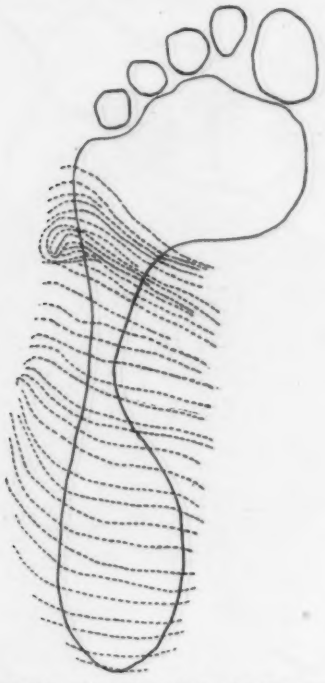

FIG. 23. Tracing of No. 178, a Negro boy, with an unusually primitive hypothenar pattern. The loop, which is unusual, has become bent backwards, or recurved, leading towards the still more primitive one shown in Fig. 24, which has almost become a whorl.

two, and a patch of ridges in a different direction. That is precisely what we do find, if we take the precaution to print a separate piece of paper, by first inking the inner curve of the foot directly, and covering it with the piece of paper. In the majority of cases the result is negative, but occasionally there is some remnant of a pattern, and this is exactly what one would expect, quite frequently a loop, either with or without a triradius, and

always drawn with very fine and soft ridges. The difference in this feature between members of the European race, on the one hand and Japanese and Chinese on the other is sufficient to serve as a racial criterion, for the almost entire absence of any trace of such a pattern in the latter, and the frequency of some trace in the

FIG. 24. Left hypothenar pattern of the foot of No. 1107. In this boy who is of the European-American race, the pattern has gone in the same way as in the Negro boy (No. 23), and has produced the nearest pattern to a whorl that has yet been found in any race.

former is very striking, as is shown in tabular form in my recent paper on the Chinese and Japanese (*Journ. Phys. Anthrop.*, Vol. V., No. 2, p. 203, 204).

The calcar pattern completes the study of the feet. This is of rare occurrence in any race, but has been observed in several

cases. It occurs about once in every hundred individuals among our people, and is usually in the form of a large loop, covering almost the entire heel, opening to the tibial side (Fig. 26). A triradius is usual, though not necessary, lying near the curve of the loop. I have met with this pattern a few times, notably in each of a pair of duplicate twins, as was to be expected. Natu-

FIG. 25. Foot of No. 87, showing the thenar pattern in the form of a closed loop. One triradius is plainly visible, the upper one belongs on the curve of the loop, and its position is sketched in (dotted line). The third, which is necessary to transform the figure into a whorl, is indicated by the convergence of the lines of the loop. That this figure is not a misplaced calcar pattern is shown by the fact that in this same foot there is a normal calcar pattern, of which the end is shown by the convergence from the other side of the ridges that come around the heel. The friction-ridge configuration is taken directly from a print, but the foot outlines are conventional, and serve to show the position of the pattern.

rally it would be most unexpected to find this pattern in the form of a complete loop, but one such case has been found, in the foot of a university professor (Fig. 27).

The morphology of the calcar pattern is still uncertain. It occurs on the calcar projection of the heel, which is distinctly human, and is unrepresented in the foot of any of our other Primates, even the anthropoid apes. One theory identifies it

with a pattern in the form of a loop, which is quite constant in the lower anthropoids, but the feet of these forms, although carefully studied, has not been treated with the basis of the walking-pads as a background and is not wholly satisfactory. Another theory links it with the hypothenar, and treats it as a component part of an enormously extended pattern, like the one reported in a few

FIG. 26. A typical calcar pattern in its usual form, that of a loop, with the head of the curve fibular, and opening (*i.e.*, converging) towards the tibial side. From life, No. 1128, pattern drawn in with help of prints.

cases, mainly of negroes, which covers almost the entire sole, back of the ball. It is also conceivable to connect it with the vestiges of the thenar. The finding of a complete calcar pattern, as in Fig. 27 goes a long way towards the determination of the calcar as an independent pattern, distinct from all others, and developed secondarily upon the extensive human addition.

The study of comparative morphology is replete with instances of survivals; the persistence of organs of former usefulness later allowed to lapse from a growing lack of importance until, no longer of value, they become vestigial. The original eleven walking pads of the primitive mammalian paw, still useful and constant in pentadactylous forms like squirrels and mice, and retained in the form of whorls in the pictures sketched by the Primates in friction-ridge patterns, and faithfully representing a

former relief of pads with their surrounding skin folds and embracing triradii, and these, in spite of the high intellectual development of man, with its accompanying change in life and habits, will still occasionally crop out, not especially in those races

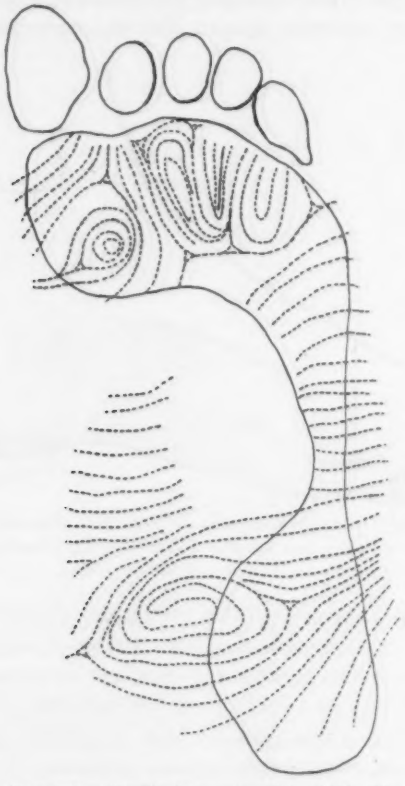

FIG. 27. Outlines taken directly from sole prints of No. 887. This sketch is taken from several prints, lapped over so that they will meet, and spread out flat. This device is rendered necessary in order to express on a flat surface the details of a curved one.

commonly considered low and bestial, but are found quite as frequently in peoples of the highest culture, and appear in primitive form now in the foot of a university professor, or in the hand of the daughter of a New Hampshire bank president, of a

New York finger-print expert, or of the author of this paper. It is true that one of the most primitive illustrations was found in a native Liberian soldier, but equally primitive cases, both in hands and feet, occur among the students of Smith College.

In my rather limited collection of peoples generally considered primitive, and including Ainus, Bontoc Igorots, Negritoes, and African Pygmies, I have found no cases that compare for primitiveness with those I have figured, which, with a few exceptions, were all of the European-American race. In some cases, if not in all, however, the lack of primitive characters has been undoubtedly due to the small number of individuals in these exotic cases, although, in the cases of the Japanese and Chinese, I was enabled to consult a sufficient number of cases to bring out unusual cases if there were any. Still, we know as yet too few individuals of any race, even of our own, to draw any sweeping conclusions from them, and it is best to treat the cases here presented as individual rather than racial.

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In my paper of 1916, published in this magazine, I endeavored, as was fitting a relative new subject, to make the bibliography as near complete as possible. Since then, with the added interest in this field, the task of keeping even the titles complete is quite beyond me, and nowhere near as possible as it was nine years ago. Here I may content myself with adding a few of the most recent titles, from the bibliographies in which one may obtain the later literature.

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MORPHOLOGY AND LIFE HISTORY OF *POLYTOMELLA CITRI* SP. NOV.

J. McA. KATER,

UNIVERSITY OF CALIFORNIA AND PRINCETON UNIVERSITY.

The organism dealt with in this paper was first found in Berkeley, California, during January, 1924, in a culture medium for *Euglena gracilis* made after Zumstein which contained the following parts: peptone .5, citric acid .2, grape sugar .5, $MgSO_4 \cdot 7H_2O$ .02, KH_2PO_4 .05, water 100. In September, 1924, a culture was shipped to me in New Jersey, from Berkeley and the cultures made from this material are still in good condition.

A little observation showed that this flagellate reproduces very rapidly during the active stage and also that an abundance of resting forms are periodically present. These facts seemed to indicate possibilities for studying the life history. Since no previous account of this organism has appeared, the name *Polytomella citri* is proposed for it.

I wish to thank Professor C. A. Kofoid for the many courtesies extended to me while working in his laboratory, Professor E. Newton Harvey for many valuable suggestions, and Professor E. G. Conklin for his constant guidance and advice.

METHODS.

Polytomella citri thrives on the medium mentioned above, but it does not make a lasting culture, two weeks usually being the limit. The best results were obtained from uncooked timothy hay in distilled water, to which a little sugar was occasionally added. An old culture can easily be renewed by dilution with distilled water. Successful cultures can be made on media with P_h value ranging from 3.5 to 9. The P_h of old hay cultures is always around 5.5 which seems to be the ideal value for this protozoan. On several occasions fresh cultures were placed in a refrigerator. After remaining there for two months the jars were fairly teeming with *Polytomella*.

During the early part of the work the cultures contained in addition to *Polytomella*, *Glaucoma scintillans*, *Chilomonas paramecium*, *Euglena gracilis*, *Bodo* sp. and some mold, but after several months everything disappeared except *Polytomella* and the mold. Zumstein's medium showed only *E. gracilis* mold, and *Polytomella citri*, the acidity of this solution being too great for the others.

The active forms were fixed in hot Schaudinn's fluid and stained in hot iron-alum-hæmatoxylin. Methyl green and Delafield's hæmatoxylin were also used, but with rather poor results. For counterstaining Bordeaux red, eosin, methylene blue, and orange G were employed, the first two yielding by far the best results. Eosin was used in the 95 per cent. alcohol, while when Bordeaux red was the counterstain the slides were placed in a 0.1 per cent. solution of the dye for twenty-four hours, immediately after applying the hæmatoxylin. Bonney's triple stain was tried, but was found to have little value for this work.

Most of the preparations were made by pipetting a drop of the culture fluid onto a slide, which had been previously smeared with a little albumen fixative, permitting this to evaporate until it did not run and then dropping slide in Schaudinn's for two minutes. Although this technique was quite successful even better results were gotten by centrifuging the material and fixing before pipetting onto the slides.

It was found that the encysted forms did not fix well in Schaudinn's nor was it possible to get them to take any kind of stain, even aceto-carmine failed to leave any trace of color. The successful technique finally developed was fixation in Bouin's or McClung's modification of Bouin's for from twelve to twenty-four hours, followed by dehydration and imbedding in paraffin. Sections were cut from two to four micra thick, and stained as above. Schaudinn's fluid was tried in place of Bouin's, but usually resulted in shrinkage of the protoplasm away from the cellulose wall.

Morphology.

Polytomella citri is a colorless flagellate of pyriform shape, the anterior end being rounded, the posterior rather bluntly pointed. The size varies from 14 by 10 micra to 10 by 7, while the average

dimensions are 12 by 8 micra. Although the body of living individuals is usually pear-shaped, the form can readily be changed. Thus we find some whose width is greater than their length, others with their posterior ends split into two or more pointed processes (Figs. 2, 3 and 4). In the latter case a groove extends forward for some distance from the notch between these processes. An optical cross-section of the typical form would be circular.

The cell is enclosed in a very thin pellicle. This covering is not visible in life and it divides with the body at fission. It is also to be noticed that it is not sufficiently rigid to prevent considerable changes of shape (Figs. 2 to 4). However, its presence can be demonstrated by dissolving the contents of the cell with dilute NaOH. When this is done the pellicle can be seen, providing the light is cut very low. In some cases plasmolysis causes the protoplasm to shrink away from the wall, thereby serving as a demonstration of its existence, but it requires very careful manipulation. The composition of this covering could not be determined, but since the heavy wall which develops around the cyst was found to be cellulose it is presumed that this has the same chemical constitution.

At the center of the anterior end are two very noticeable basal granules from which arise four equal flagella. These are slightly shorter than the body and do not taper at all, being as large at the free end as at the point of insertion. The two pairs of flagella are well separated in the living organism by a small cytoplasmic protuberance which extends forward between the basal granules (Fig. 1). This prominence is never preserved after fixation.

The two contractile vacuoles are located at the anterior end. They pulsate alternately.

The spherical nucleus is about 3 micra in diameter and is situated at any point along the long axis of the cell from the posterior fourth to the anterior fourth. All of the chromatin is concentrated in a central sphere, the karyosome. This body is anchored to the nuclear membrane by an indefinite number of achromatic strands. Six is the greatest number of these supports that have been seen, four the least. Aside from the strands the space between the karyosome and membrane is optically empty.

Surrounding the nucleus is an area of very granular, slightly chromatic cytoplasm. This is of very variable extensiveness, sometimes filling half of the cell, while in others it is hardly noticeable.

Examination of living specimens reveals longitudinal striations which number about eighteen. It was not possible to make sure of the exact number and consequently their constancy could not be determined. Superficial examination would lead one to think that these were on the outside of the pellicle, but careful focusing shows that they are slightly below the surface and that they do not quite reach either the anterior or posterior ends. They, consequently, must be either on the inside of the pellicle or in the outermost layer of the ectoplasm. After devoting considerable study to this question I rather lean towards the latter, and think that the striated effect is produced by some stringy arrangement of the protoplasm. Living mounts or iodine-eosin preparations show this structure very well, but fixed and stained material gives no indication of it.

In the living cell all of the internal structure is effectually screened by relatively large starch bodies which are located peripherally. They may be so large and numerous that they are packed closely together from one end to the other or they may be entirely absent. By the use of a medium which does not contain any carbohydrate (peptone 0.5 part, citric acid 0.2 part, magnesium sulphate hydrate .02, KH_2PO_4 .05 part, and water 100 parts) the organisms may be freed from starch for several days, when it reappears again. No explanation of this fact is known. The addition of cane-sugar to a timothy hay culture will increase the amount of reserve starch in the cells. If they are only partially filled with these bodies it is generally the posterior end which is free from them.

The following reactions are the justification for identifying this material as starch; it gives a deep blue color when treated with iodine; it is digested by ptyalin; when treated with iodine and heated it loses its color, the blue returning when cooled; when treated with iodine followed by NaOH no color is found.

The presence of a centriole could not be demonstrated in the interkinetic cell of the active form. However it was seen in

several of the division stages figured in this paper (Figs. 13–15). Sections of cysts showed a centriole very clearly.

In the active forms an indication of rhizoplasts connecting the basal granules with the nucleus was seen in a few cases (Figs. 20 and 24). This, however must remain purely tentative until more evidence can be produced. There is no doubt as to the presence of this structure in the cyst just previous to excystment (Figs. 38–40). Whether it degenerates after excystment or merely was not demonstrated because of faulty technique, or for other reasons, cannot be decided.

Scattered through the cytoplasm of the active form there are sometimes seen a few very basiphilic granules. These stain even darker with iron-alum-hæmatoxylin than does the nuclear chromatin, and also give the typical reaction with Bonney's triple stain and methyl green. They increase to such an extent in the cyst that during part of that stage they effectually obscure the entire contents of the cell. For reasons which will be discussed later these are termed metachromatic granules.

Seven individuals with two nuclei have been seen. They probably represent cases where fission was prevented, by some unknown reason, from following mitosis.

When the resting condition is entered the flagellates cease movement, lose their flagella, round up into a perfect sphere and secrete an extremely thick wall (Fig. 26). From this early spherical stage they pass into an indefinitely wrinkled condition, which must result from drying of the cell contents (Figs. 28 and 29). A gradual disappearance of the starch bodies can be traced and correlated with the wrinkling of the cyst. Chloro-zinc-iodide and sulphuric acid followed by iodine both indicate the wall to be composed of cellulose.

Life History.

So far as could be determined the life history consists of two phases, (1) active life and (2) rest and reorganization through encystment. During the time of activity *Polytomella* reproduces by means of longitudinal fission. No multiplication whatever takes place during the period of rest. This is well established since hundreds of stained specimens have been examined and

many living ones watched continuously during the process of excystment without the slightest evidence of propagation. *There is no indication of a sexual phase in any part of the life cycle.*

Mitosis.—By far the greater number of flagellates in which mitosis has been studied possess within the nucleus an endosome and, surrounding this body, scattered chromatin granules. It is from this scattered material that the chromosomes are usually formed. In Polytomella citri we have a different story, all of the chromatin being located in a single central body, the karyosome [1] (*Parapolytoma satura* has a very similar nucleus, Jameson, 1916).

The orderly behavior of the karyosome during the early part of the prophase is very interesting. The first indication of mitosis is the bisection of this body in a plane transverse to the long axis of the cell-body. The two parts appear to be equal and they pull slightly apart, leaving between them a light cloud. A second division follows the first and forms at right angles with it. The karyosome now consists of four parts which still have the chromatic cloud between them. In the next stage that could be found eight karyosomal bodies, imbedded in the chromatic cloud, were visible. Since the karyosome is spherical we would expect a division, corresponding to the third cleavage of a fertilized egg, between the last two. It may be that such is the case, but the minute size of the objects made it impossible to determine. The division of the karyosome continues until more than twenty particles can be made out, still imbedded in the chromatic cloud. It is interesting to note that the anchoring strands are still persisting. Careful observations were made in an attempt to determine whether they connected, internally, with individual granules or were a part of some achromatic supporting structure within the karyosome, but without results.

In the next step the chromidial cloud lightens, the nucleus becomes transversely elongate to a slight extent, there is a condensation of the numerous small granules and a spireme appears. This consists of seventeen or eighteen chromatin bodies connected by slender achromatic strands. When the nucleus lengthens

[1] There is no question concerning the nature of the chromatic body within the nucleus of *Polytomella* and since karyosome has a more restricted meaning than endosome it can well be used here, though I consider that endosome, as suggested by Minchin, is a valuable term for the nucleoli of many protozoan nuclei.

more and an indication of a spindle appears the chromatin knots on the spireme have been reduced in number to nine and have increased considerably in size. It cannot be said whether this results from the side to side pairing of the eighteen earlier granules or the contraction of alternate connecting strands as evidence was found for both. The achromatic connections still exist between these, the definitive chromosomes. The spireme is now near the equator of the spindle, and in all later stages the strands between the chromosomes have disappeared. The last figure which can be classed as prophase shows the chromosomes lining up on the equator to form a horse shoe around the spindle. The chromosomes which are first freed from each other by the disappearance of the strands are considerably longer than they are broad. The length is quickly reduced, so that when they split at the metaphase the two daughter chromosomes resemble two balls that are in contact. Several very clear polar views of the metaphase were found which indicated the number of chromosomes to be nine. These are arranged in the horseshoe-shape which was noted in side view.

As noted above a centriole could not be demonstrated in the resting cell. With the elongation of the nucleus and formation of the spindle in the late prophase a granule appears at the poles of the spindle (Figs. 13–15). On the anterior side of the nucleus a line connecting the poles is seen on the nuclear membrane. This, which we shall tentatively term a paradesmose, becomes much more striking in the later stages. Hesitancy in definitely naming this structure is due not to doubt concerning its occurrence, but to the inconclusive demonstrations of a constant centriole, which, presumably, would give rise to the paradesmose.

With the progress of the chromosomes towards the poles the spindle widens to equal the diameter of the horse shoe of chromatin until the band has traversed two thirds of the distance to the poles. Some of the chromosomes now advance ahead of the rest, which show a tendency to clump together. At the same time the nuclear membrane is beginning to constrict at the equator. A little later the dividing nucleus is drawn out into a cylinder with pointed ends, and the chromosomes are clumped into several masses at the ends of the slender cylinder. With the

cylindrical shape of the nucleus comes an enlargement of the basal granules, preparatory to their division which will take place just before constriction of the nucleus is complete. At this time the chromatin is clumped into a single mass. The two basal granules divide to form four, each of which gets one of the old flagella. Although no unquestionable figures were found which showed the outgrowth of new flagella it is presumed that this is the method of formation, because if the old flagella split we would expect that to happen at the same time that the basal granules divide and that is not the case. The duplication is by outgrowth in *P. agiles* (Doflein, 1916), *Dunaliella* (Teodoresco, 1905), *Stephanoptera* (Dangeard, 1910), all belonging to this same family.

The history of the chromatin from the beginning of the telophase, when there are single masses at the poles, until the construction of the daughter nuclei is complete is a rapid return through the same stages in reverse order that were passed through in the prophase. The solid masses break up to form a spireme which goes back through the quadri- and bi-partite karyosome to the single condition with which we started. By the time the quadri-partite condition of the karyosome is reached the cell shows marked furrows on both the anterior and posterior ends. In most flagellates fission has been described as beginning at one or the other end. The present case is an example of equal furrowing all around the cell-body. The resting condition is reached by the nuclei, or is very closely approximated, by the time fission is complete. It is interesting to note that the two daughter nuclei are frequently not advanced to the same degree.

We must now return to the first elongation of the nucleus and find what happens to the area of dense cytoplasm which surrounds the nucleus. A glance at the figures from metaphase on will show that there is a fairly even distribution of this material to the daughters. Sometimes it surrounds the nucleus in an even layer, in others it is almost all on one side, and in rare cases it is slightly drawn away from the nucleus. A band of this substance can be seen stretching between the daughter nuclei just before the cells separate. The chromatic nature of this material probably indicates that, although the nuclear membrane remains intact during

mitosis, there is some substance of the nature of oxychromatin that is dissolved and passes through the nuclear membrane. This would make the cytoplasmic area under discussion correspond to the archoplasm of Boveri and the archiplasm of Conklin and Wilson. There was no indication of granules of chromatin going bodily through the nuclear membrane.

Encystment.—When the cell enters encystment the cellulose wall is evidently formed very rapidly. Only a few individuals were found that did not have a perceptible membrane and in these cases it was only a matter of several hours until they looked quite old and sturdy. While the cyst is still spherical the starch bodies are well under way to disappearance (Figs. 26 and 27). When the wrinkling of the cyst has reached the degree which typically makes the general outline triangular the starch is all gone. Observation of many stained sections of early spherical cysts did not reveal any remnant of the basal granules.

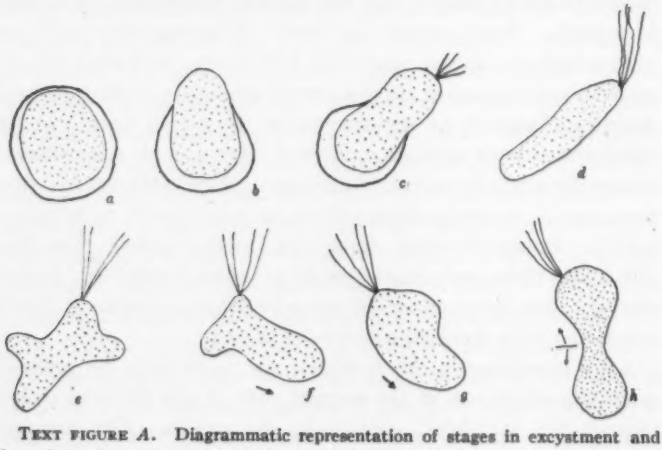
As soon as the organism has become encysted the region immediately surrounding the nucleus becomes filled with spherical bodies which are more basiphilic than the nucleus itself. These bodies increase in extent with the aging of the cyst and soon come to fill the entire cell. In many cases the nucleus, which has now decreased to half its original size and stains very faintly, is obscured. Unless a study of this stage is made very critically one might be led to believe that the nucleus has broken up to form chromidia. Such is not the case. Whenever the knife cut through the nucleus or near it the karyosome, anchoring strands, and nuclear membrane make a perfect miniature, in both size and staining character, of the nucleus of the active form. In the hundreds of such sections examined there was no suggestion of chromatin particles leaving the nucleus. Since this material does not come from the nucleus and stains more deeply with hæmatoxylin, Bonney's triple stain, and methyl green than does chromatin the name metachromatic granules is justified. It is of interest that the increase of metachromatic granules is highly correlated with the disappearance of starch.

After remaining in this condition for some time the granules gradually drain out of the central part of the cell and collect around the periphery, mostly in the angles. The previous

spherical form is lost and they assume various shapes. In most cases they entirely disappear before excystment.

When the metachromatic granules are distributed through the entire cell with only small dots of cytoplasm visible, acid dyes, such as Bordeaux Red and eosin, have no effect on what cytoplasm can be seen, even when extra high percentages are used. With the migration of the granules to the periphery the cytoplasm regains its affinity for acid dyes.

After the metachromatic granules have left the immediate vicinity of the nucleus and the cytoplasm has become quite clear we get the first indication of a new centriole and basal granule, in the form of a thickening at the base of one of the anchoring strands. This thickening next appears as a chromatic ball on the strand, a part of which can be seen on each side of the ball. Later it continues to the outside of the nuclear membrane. The basiphilic material that has been drawn out of the karyosome leaves the latter body without disfiguring it. Thus we see that the centriole and basal granules are not formed from a slice of the karyosome, but are taken from that structure by some definitely organized scheme. The body on the outside of the nuclear membrane divides, leaving one portion, supposedly the centriole, while the other portion migrates out through the cytoplasm, spinning a rhizoplast between it and the centriole. Before



TEXT FIGURE *A*. Diagrammatic representation of stages in excystment and the activity of a newly excysted individual. Arrows indicate direction of movement.

reaching the periphery the single basal granule divides, the rhizoplast dividing with it, to form the two basal granules. The flagella do not develop until the organism is partly excysted.

Excystment is ushered in by the dissolution of the cyst wall on one side (Text Fig. *Aa*). Many stages of this thinning process can be seen before the living cell comes in contact with the outside. The first step in escaping from the cyst seems to be due to the absorption of water, which swells the cell and causes it to protrude through the dissolved opening. Complete freedom from the cyst wall is attained by amœboid movement of the newly formed flagellate. Outgrowth of flagella begins just prior to flowing away from the old wall.

For periods varying from one to fifteen minutes the newly excysted individual shows only amœboid movement, without regard for the polarization caused by the presence of flagella (Text Fig. *Ae, f, g, h*). With the cessation of amœboid movement they assume the typical form and swim off.

Discussion.

Affinities.

The presence of starch within the cell-body of *Polytomella citri* and the typical Phytomonad symmetry are sufficient to establish its position with the order Phytomonadina. Further, the fact that the pellicle divides with the cell at fission places this organism within the family Polyblepharididæ.

This family was suggested by Dangeard in 1887 to include, at that time, *Pyramimonas tetracynchus* Schmarda, *Chloraster gyrans* Ehrenberg, *C. agilis* Kent and *Polyblepharides singularis* Dangeard. In 1905 Teodoresco placed *Dunaliella salina* in this group. This is a marine protozoan, as the name would indicate. Griffith (1909) described *Pyramimonas delicatulus*, taken from a pond in England. In 1910 Dangeard made another contribution to the Polyblepharididæ with his description of *Stephanoptera fabreæ*, a salt water form. This species is one of the largest of the family, reaching 35 micra in length. *Pyramimonas*, 40 micra, being the only one exceeding that size. All of the members of this group possess the ability to change their shape to some extent and *Spermatozopsis exsultans* (Korchikoff, 1913) has the dis-

tinction of leading the family in this respect. *Astermonas* was the last holophytic genus described (Artari, 1913).

Dangeard instituted this family to include holophytic, unicellular algæ and all of the species mentioned above would fit in with that scheme. They possess a chloroplast, a pyrenoid for the formation of starch, and a red pigment spot may or may not be present. In *Dunaliella* the green is sometimes obscured by another pigment which gives the organism a vermillion color.

A phylogenetic series might be made, beginning with the six or eight flagellated Polyblepharides, going through the five flagellated *Chloraster*, *Pyramimonas*, which possesses four flagella, *Stephanoptera*, with two flagella, and culminating with the biflagellate *Dunaliella*, the nearest approach to *Chlamydomonas*. With the exception of *Dunaliella* all species have four longitudinal ridges. One might suggest that the scheme could be arranged in the opposite direction, but since the specialization of the Chlamydomonad type is much greater than that of the Polyblepharididæ this order seems the more reasonable.

In 1910 Aragao described *Polytomella agilis* and suggested that ts relationship was with the Protomonads. Doflein (1916) demonstrated the presence of starch in the same species and consequently, reclassified it under the order Phytomonadina, and since its pellicle divides at fission its family is Polyblepharididæ. This colorless form, possessing four flagella, stands in the same relation to *Pyramimonas* that *Polytoma* and *Paraplytoma* do to *Chlamydomonas*. Dangeard's family no longer includes only holophytic algæ, and the green color must be omitted from a characterization of it.

The protozoan dealt with in this paper differs from Aragao's species in the following points: an eye-spot is present in *agilis* while *citri* possesses no such structure; the nucleus of *agilis* contains scattered chromatin while in *citri* it is concentrated in a single karyosome, the four flagella of *agilis* arise from four blepharoplasts and *citri* has only two basal granules. These differences are not sufficient for generic distinction, but justify the formation of a new species.

It is to be regretted that so little study has been made of the finer points of structure of the members of this group, the

importance of which must be realized when we consider its position on the threshold of the Phytomonadina.

Life History.

With the exception of *Polytomella agilis* and *Dunaliella salina* the descriptions of the members of this family would lead us to believe that the life history consists of two phases, binary fission during the active stage and rest and reorganization through encystment. Dangeard (1889) describes the cysts of *Polyblepharides* as spherical bodies with a gelatinous wall. This is the only one which has such a covering. To the same author is due the observation that *Pyramimonas* forms cysts with a very tough membrane. Germination of the latter was not observed, but in the former it gave rise to a single organism, which, after exhibiting typical amœboid movement for several minutes would assume the usual shape and swim off by the activity of their flagella. This same observation was made on *Polytomella citri*. Hamburger (1905) noted the formation of cysts by *Dunaliella* and also saw numerous empty shells but did not observe any in the process of excystment. The cysts of *Stephanoptera* are spherical and have a very heavy wall. Dangeard mentions the fact that a few of these had two nuclei, and suggests that there may be some autogamous process during encysted life. The binucleate condition, however, probably does not have any more significance here than it does in the active stage of *Polytomella citri*, where we have interpreted it as representing cases of cytodierisis being prevented from following nuclear division.

Conjugation has been figured by Aragao for *Polytomella agilis* and by Teodoresco for *Dunaliella*. In both cases the figures and description are very incomplete and unconvincing. There are none of the few figures given that could not more easily be interpreted as stages in fission than as representing conjugation. This is especially true for the work of Aragao. In spite of the fact that sexual reproduction probably plays no part in the life of most of the members of this family, we would not be surprised to find sexual processes in *Dunaliella* because of its near relationship to *Chlamydomonas*. However, until a more adequate study has been made with this problem in view it is well to be hesitant in

accepting the Polyblepharididæ as the group which gave rise to the sexual phenomena which are so well developed in the two higher families of the Phytomonadina.

Mitosis.—The nucleus of most flagellates contains, in addition to the endosome, scattered chromatin granules which seem to be suspended on a linin net-work. The rôle of the endosome in nuclear division is generally one of two types. The first, typified by the Euglenoids, is the case where this body is drawn out into a dumbbell shape, in the interior of the spindle, with the two knobs forming polar caps. With the progress of the chromosomes to the poles this structure is severed at the equator and forms the endosomes of the daughter nuclei. Some writers (Belar, 1916*A*, Berliner, 1909, Schussler, 1917) have termed this central body of the Euglenoid a "centrocaryosome," assigning to it the function of a centrosome. Hall, however, has questioned this view. Another type of behavior is illustrated by the endosome of *Polytoma* (Entz, 1918) and *Chlorogonium* (Hartmann, 1916) which disappears during the prophase. Aragao described the formation of two sets of chromosomes in *Polytomella agilis*, one from the scattered chromatin, the other from the endosome. Doflein (1916), repeating his work, found that the endosome disappeared during the prophase without contributing to the formation of the chromosomes.

It is very evident that a comparison cannot be made of the mitotic phenomena of *P. citri* and those of any form just mentioned, not even the other species of its own genus. However, a similar form is found in *Parapolytoma satura* (Jameson, 1914) which has all of the chromatin gathered into a single body, the karyosome, which is suspended from the nuclear membrane in much the same way as in *P. citri*. Unfortunately Jameson's account begins rather late in the prophase, his first figure showing the karyosome broken into a number of bodies which are connected by linin strands. He states that the greatest number of these ever found is sixteen or eighteen, which fuse in two's or three's to form the eight definitive chromosomes. The same behavior has been found in *P. citri*, with the addition of the early stages in the fragmentation of the karyosome. Although the chromosomes of *P. agilis* are formed from scattered chromatin the

five definitive ones arise in much the same way, by the pairing of ten chromatin granules which form a ring around the endosome. Doflein analogizes this fusion with the conjugation of homologous pairs of chromosomes in metazoan and metaphytan cells.

Thus we see that the greatest similarity in the activity of two cell-organs is not to be found in two organisms whose general structure is most nearly alike, but in two that have the nearest approach to identity in that particular organ.

Encystment.—There is a remarkable correspondence of the encysted forms of the various species of this family. *Pyramimonas delicatulus* and *Spermatozopsis exsultans* are the only ones in which cysts have not been described. There is only one case where division takes place within the cyst (Doflein, 1916). Aragao did not find division in this same species. This author met with the same difficulty that was encountered in the present work, namely, that the cyst could not be stained. This fact is probably responsible for the fragmentary study of this important phase of the life history of the Polyblepharididæ, as no adequate account has heretofore appeared.

In *Polyblepharides* and *Polytomella citri* the living organisms have been watched during excystment and in both cases amœboid movement was observed for some minutes before any use was made of the developing flagella. *Dunaliella* and *Polytomella citri*, and probably all of their near relatives, leave the cyst wall behind without dissolving it. The latter dissolves on one side in order to gain freedom, but the remainder of the shell stays in the culture for some time.

Since the pioneer work of Guillermond and Meyer metachromatic granules have been described from bacteria to metazoa. The fact that these granules not only increase greatly during the early days of encystment, but also are dissolved, not thrown off, before excystment indicates that they have some important rôle to play in the life of *Polytomella citri*.

Centriole and Basal Granules.

The observations made on this subject in the present work are as follows: There are two basal granules from which arise four flagella. These granules divide during the telophase of mitosis.

The poles of the spindle are lodged in centrioles which are located on the outside of the nuclear membrane. An indication of rhizoplasts connecting the basal granules with the nucleus have been seen in both resting and dividing cells. In the early cysts no basal granules can be seen. Before excystment a centriole and new basal granules arise from the karyosome. This material is drawn out of the latter body without disfiguring it. There is, at first, a single basal granule which divides before reaching the periphery. A rhizoplast is very evident during this phase. The new flagella grow out after the organism is partly excysted. The questions not answered are: is a centriole present in the resting cell of the active form; what becomes of the rhizoplasts that are so evident before excystment; are the basal granules drawn into the karyosome at the beginning of encystment or do they degenerate?

In view of the fact that a centriole can be seen in division stages, is very pronounced in the cysts and that Doflein has demonstrated an extra-nuclear centriole in *Polytomella agilis* I think we can conclude that such a center is present in the interkinetic cell of *P. citri.* In addition the paradesmose, which is quite evident, would, presumably, come from a centriole. Jameson (1914) says that *Parapolytoma* has no centriole. He mentions *Chilomonas* and *Polytoma* as other examples of flagellates without this division center. It is to be noted that Belar (1916) demonstrated a centriole in *Chilomonas* and Entz (1918) showed that *Polytoma* has a very definite one on the inside of the nuclear membrane, with a heavy centrodesmose appearing at division.

Aragao figures rhizoplasts connecting the basal granules of *P. agilis* with the nucleus. Hamburger did likewise for *Dunaliella.* In view of these observations, coupled with what has been seen in *P. citri* I believe we are justified in assuming that the rhizoplasts are constant structures in *P. citri.*

Berliner states that the basal granules of *Copromonas* are drawn into the endosome at division. His figures, however, are not at all complete. Jameson finds that the basal granules of *Parapolytoma* never divide, but three of the four individuals resulting from division receive new basal granules from the karyosome. Entz finds that the centriole and blepharoplasts of *Polytoma* arise

in the same way as in *P. citri* with the exception that the centriole remains inside the nuclear membrane. Although it is impossible to definitely answer the third question suggested above, it seems more probable that the granules degenerate because if they entered the karyosome we would expect them to maintain their integrity to sufficient extent to prevent the karyosome from appearing perfectly homogeneous. Such is not the case.

Summary.

The flagellate herein described belongs to the genus *Polytomella* (Aragao, 1910). The specific name "*citri*" is proposed. The size ranges from 10 by 7 micra to 14 by 10 micra. Outside of the absence of chlorophyll the structure is typical for the family Polyblepharididæ. Although it is a colorless, saprophytic organism the cell-body contains numerous starch bodies.

The life history consists of active stage, in which reproduction is by binary fission, and encystment. No reproduction takes place during encystment. There is no indication of any sexual process at any point of the life cycle.

Conjugation is not well established in any species of the family.

The chromosomes arise as a result of the fusion of chromatin particles which have come from the karyosome.

The cysts are filled with metachromatic granules. They usually disappear before excystment.

A new centriole and basal granules are given off from the karyosome previous to excystment. Flagella do not grow out until the cell comes in contact with the outside. Amœboid movement is the means of locomotion for several minutes following excystment.

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EXPLANATION OF PLATES.

Figures 1 and 25 to 29 made from living material. Figures 2 to 24 made from material fixed in hot Schaudinn's fluid and stained in hot iron-alum-hæmatoxylin, counterstained with Bordeaux red. Figures 30 to 41 were made from specimens fixed in Bouin's, stained in hot iron-alum-hæmatoxylin and counterstained with either Bordeaux red or eosin. All drawings made with Abbe camera lucida. Magnification 2500 X.

PLATE I.

FIG. 1. Diagrammatic camera lucida drawing of living individual pressed between two mold hyphæ. *cv*, contractile vacuole; *s*, starch bodies.

FIGS. 2, 3 AND 4. Showing extreme changes of shape.

FIG. 5. Binucleate individual.

FIG. 6. Resting nucleus. Extensive area of slightly chromatic cytoplasm surrounding nucleus and filling posterior end.

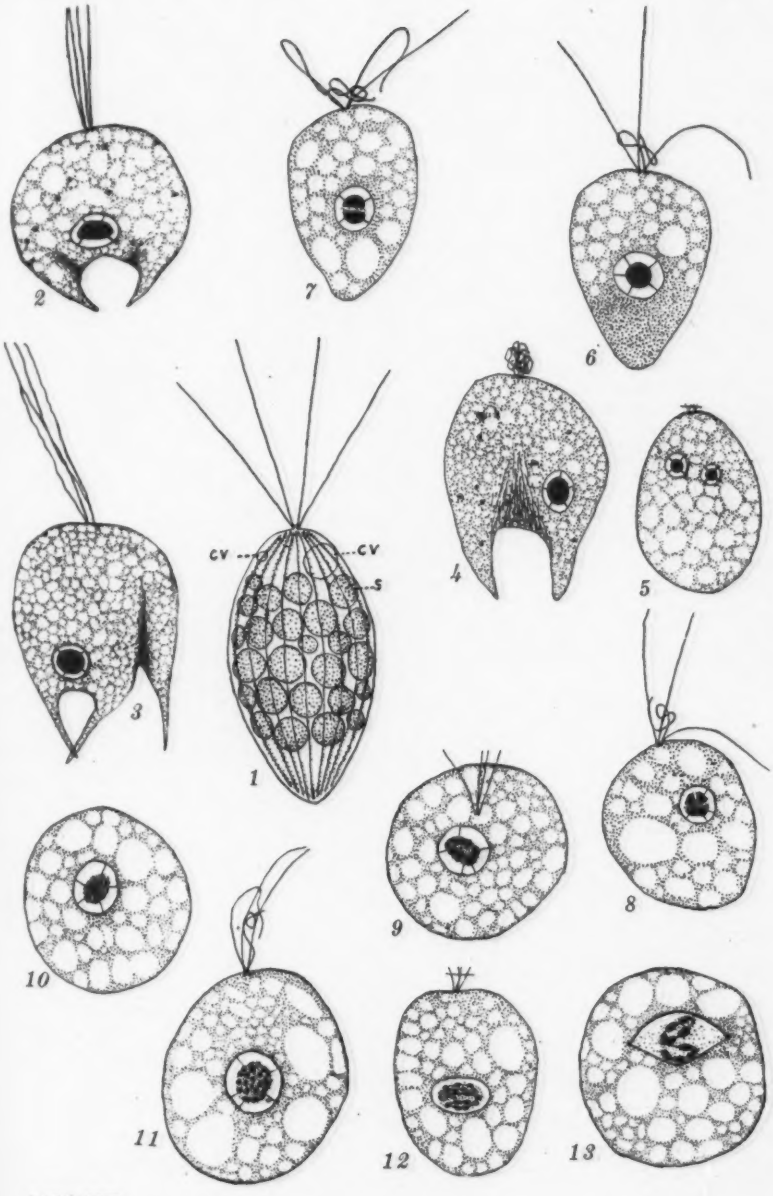
FIGS. 7 TO 24. Stages in the division of the nucleus and cell-body.

Fig. 7. The transverse splitting of the karyosome, the first indication of mitosis.

FIGS. 8 TO 11. Continued fragmentation of the karyosome resulting in over twenty chromatin particles imbedded in a chromatic cloud. Anchoring strands persisting.

FIG. 12. Nucleus becomes slightly elongate, anchoring strands disappear, and seventeen or eighteen chromatin particles connected by slender achromatic strands become visible.

FIG. 13. The chromatin particles of the preceding one have paired to produce the nine definitive chromosomes. An indication of a spindle appears and the poles are lodged in centrioles which are connected by a paradesmose on the anterior side of the nucleus.



J. McA. KATER.

PLATE II.

FIG. 14. Chromosomes lining up on equator to form horse shoe around the spindle. Paradesmose visible above spindle.

FIG. 15. Metaphase.

FIG. 16. Polar view of metaphase.

FIGS. 17 AND 18. Migration of chromosomes to poles of spindle.

FIG. 19. The nucleus has become elongated into a cylinder with pointed ends and the chromosomes are fusing together. The paradesmose is seen on anterior side of nuclear membrane and the basal granules are enlarging.

FIG. 20. The chromosomes have fused into a single mass at the poles, and the basal granules have divided.

FIG. 21. The chromatin masses of the preceding one have broken up to form a spireme comparable to that of Fig. 13.

FIGS. 22 AND 23. Reconstitution of the daughter nuclei and division of the cell.

FIG. 24. A case where fission was either delayed or prevented by some unknown cause.

FIG. 25. Beginning of encystment. The flagella have been lost and the cell is packed with starch bodies.

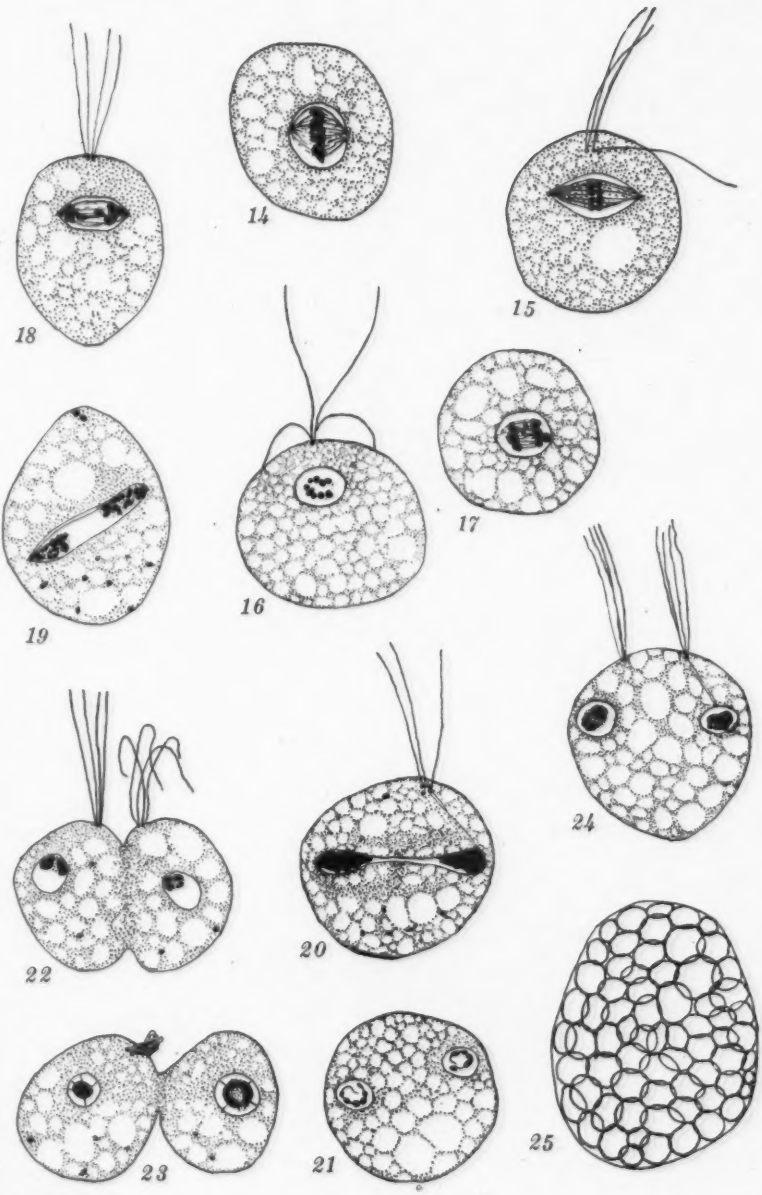


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PLATE III.

FIGS. 26 TO 29. Stages in the formation of wrinkled cyst wall and the disappearance of the starch bodies.

FIGS. 30 TO 40. Made from sections four micra thick.

FIG. 30. Early cyst. Metachromatic granules are forming around the nucleus.

FIG. 31. The wall has become thicker than in the preceding case and the metachromatic granules are scattered through the entire cell. Nucleus obscured.

FIG. 32. The metachromatic granules are evenly distributed through the cytoplasm. Wall becoming wrinkled.

FIG. 33. The metachromatic granules are migrating to the periphery where they will be dissolved.

FIG. 34. The first indication of budding of the karyosome. A thickening appears at the base of one of the anchoring strands.

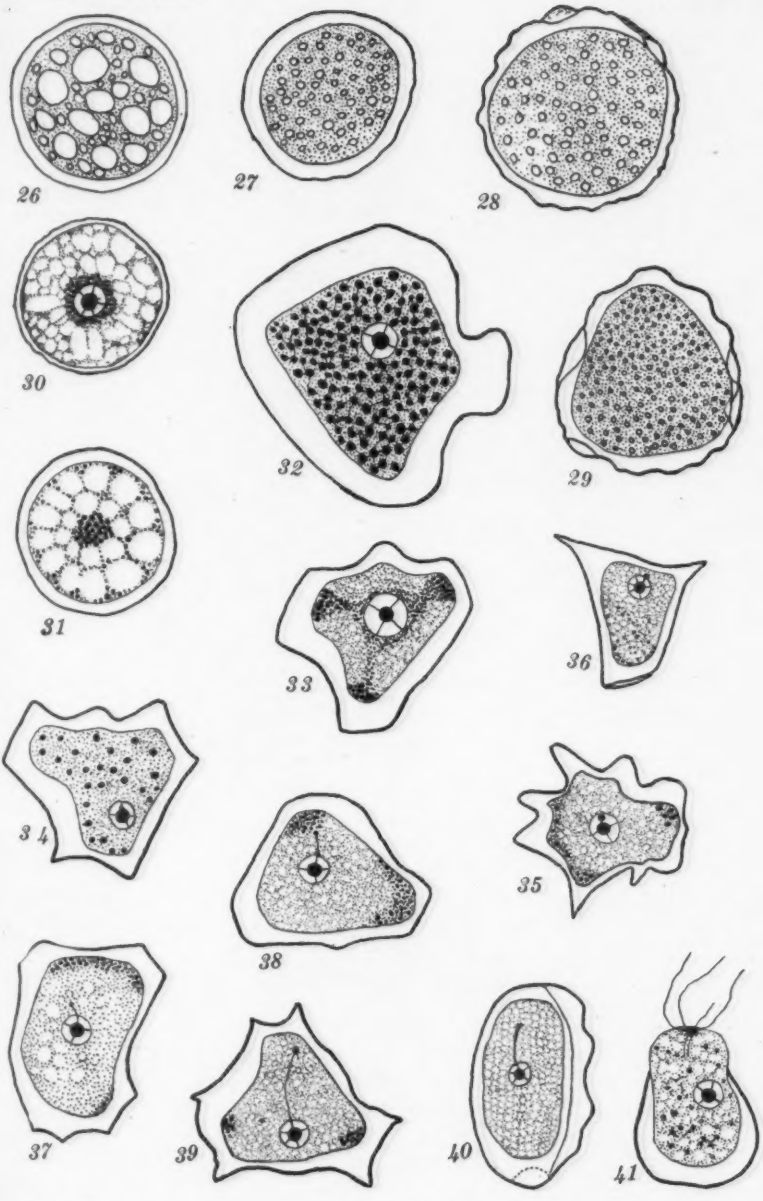
FIG. 35. The material which is going to form the new centriole and basal granules appears as a chromatic ball on one of the anchoring strands.

FIG. 36. The chromatic ball has reached the outside of the nuclear membrane.

FIGS. 37, 38 AND 39. Stages in the migration of the basal granule towards the periphery.

FIG. 40. The basal granule has divided, the rhizoplast dividing with it.

FIG. 41. Drawing made from whole mount. The organism is partly excysted and the flagella are growing out.



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